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PHÉNOLOGIE, EFFORT DE REPRODUCTION ET VARIABILITÉ CLIMATIQUE: UNE ÉTUDE À LONG TERME DE *DRYAS INTEGRIFOLIA* DANS L'ARCTIQUE CANADIEN

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AVANT-PROPOS

Ce mémoire de Maîtrise en Sciences de l'Environnement présente l'analyse d'une banque de données écologiques à long terme et les résultats de travaux de terrain effectués à Baker Lake, Nunavut, durant l'été 2005 sous la direction de Dre Esther Lévesque. Il comprend 2 chapitres : le Chapitre 1, un résumé substantiel, présente brièvement la problématique, les objectifs, la méthodologie, les résultats et les conclusions de mes travaux de recherches; le Chapitre 2 est constitué d'un article scientifique rédigé en anglais qui sera soumis à une revue à comité de lecture. L'article s'intitule "Phenology, reproduction and climate variability: a 13-year study in the Canadian Arctic". Il examine les liens entre les variations inter-annuelles du climat et celles de la phénologie et de la reproduction d'une plante vasculaire très répandue dans l'Arctique. Les informations complémentaires qui n'ont pu être incluses dans l'article scientifique se retrouvent en annexe. En annexe 1, une caractérisation approfondie d'un de nos sites est présentée (micro-climat, végétation et sol) et en annexe 2, on retrouve les résultats d'un réchauffement expérimental de la végétation à l'aide de serres ouvertes (Open Top Chambers) pendant une saison de croissance au site de Baker Lake.

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TABLE DES MATIÈRES

AVANT-PROPOS ii

REMERCIEMENTS iii

TABLE DES MATIÈRES v

LISTE DES TABLEAUX vii

LISTE DES FIGURES viii

CHAPITRE 1 1

RÉSUMÉ SUBSTANTIEL 1

1.1 INTRODUCTION 1
1.2 PROBLÉMATIQUE 2
1.3 OBJECTIFS 5
1.4 MÉTHODES 6
1.5 RÉSULTATS 10
1.6 CONCLUSIONS 12

CHAPITRE 2 13

PHENOLOGY, REPRODUCTIVE EFFORT AND CLIMATE VARIABILITY: A 13-YEAR STUDY IN THE CANADIAN ARCTIC 13

2.1 RÉSUMÉ 14
2.2 ABSTRACT 15
2.3 INTRODUCTION 17
2.4 MATERIALS AND METHODS 20
2.4.1 Research Sites *20*
2.4.2 Study Species *20*
2.4.3 Climatic data *21*
2.4.4 Phenology and flower production *22*
2.4.5 Statistical analysis *23*
2.5 RESULTS 24
2.5.1 Climate *24*
2.5.2 Phenological responses *26*
2.5.3 Reproductive effort *29*
2.6 DISCUSSION 32
2.6.1 Climate variability *32*
2.6.2 Interannual variations of phenology *34*
2.6.3 Interannual variations of reproductive effort *36*
2.6.4 Implications in context with Global Change *39*
2.7 CONCLUSIONS 41
2.8 ACKNOWLEDGEMENTS 42

BIBLIOGRAPHIE 56

ANNEXE 1 65

CARACTÉRISATION DU SITE ITEX DE BAKER LAKE 65

ANNEXE 2 : 73

EFFET D'UN RÉCHAUFFEMENT EXPÉRIMENTAL À L'AIDE DE SERRES OUVERTES « OPEN TOP CHAMBERS » (OTC) SUR LA PHÉNOLOGIE ET L'EFFORT DE REPRODUCTION DE *DRYAS INTEGRIFOLIA*..... 73

LISTE DES TABLEAUX

TABLE 2.1 Climate and vegetation characteristics (mean ± standard deviation) of the study sites,Tanquary Fiord and Baker Lake, Nunavut..... 43

TABLE 2.2 Independent variables used in multiple regressions of interannual variation of phenology (dates of peak budding and flowering and first fruiting) on climatic variables for 1990-2005 at the two study sites. 44

TABLE 2.3 Independent variables used in the multiple regressions of interannual variation of reproductive effort (number of buds, flowers and fruits) on climatic variables for 1990-2005 at the two study sites. 45

TABLE 2.4 Year to year variability (median difference between mean temperatures of two consecutive years, Δ T) and range of mean temperatures (annual and seasonal) at the two study sites for 1990-2005. 46

TABLE 2.5 Multiple regression of median date of flowering (mean from flowering dates of 30 *Dryas integrifolia* plants) on climatic variables in Baker Lake between 1992-2005. 47

TABLE 2.6 Multiple regression of median date of flowering (mean from median flowering dates of 25 *Dryas integrifolia* plants) on climatic variables in Tanquary Fjord, Nunavut, between 1994-2005. 47

TABLE 2.7 Multiple regression of first date of fruiting (mean from fruiting dates of 30 *Dryas integrifolia* plants) on climatic variables in Baker Lake between 1992-2005. 47

TABLE 2.8 Multiple regression of mean number of flowers (mean from 30 *Dryas integrifolia* plants) on climatic variables in Baker Lake, Nunavut. 48

TABLE 2.9 Multiple regression of mean number of buds (mean from 25 *Dryas integrifolia* plants) on climatic variables at Tanquary Fjord, Nunavut..... 48

TABLEAU A1.1 Recouvrement (moyenne de 30 quadrats ± SE) des composantes abiotiques et biotiques présentes au site ITEX de Baker Lake, Nunavut. 70

TABLEAU A1.2 Caractéristiques du sol au site ITEX de Baker Lake, Nunavut, sous différentes plantes. Les échantillons ont été récoltés entre 0-10 cm de profondeur et analysés à partir de la fraction fine du sol (< 2 mm). 72

LISTE DES FIGURES

FIGURE 2.1 Location of the two study sites (modified from Microsoft Map Point) and picture of each site, Tanquary Fjord (81°N)(a) and Baker Lake (64°N)(b). 49

FIGURE 2.2 Annual and seasonal temperature anomalies (centered and reduced means) for 1990-2005 at Baker Lake and Eureka (Environment Canada meteorological stations) evaluated with respect to the 1971-2000 means. Smoothed line represents results from a Type 2 Hanning low-pass filter. 50

FIGURE 2.3 Liquid precipitation anomalies (centered and reduced means) for 1990-2005 at Baker Lake (a) and Eureka (b) (Environment Canada meteorological stations) evaluated with respect to the 1971-2000 means. Smoothed line represents results from a Type 2 Hanning low-pass filter. 51

FIGURE 2.4 Mean thawing degree-days (a) and number of days with mean temperatures above 0°C (b) at Baker Lake and Tanquary Fjord. 52

FIGURE 2.5 Interannual variation of dates of peak budding, peak flowering and first fruiting for *Dryas integrifolia*. Mean dates from 30 plants at Baker Lake (a) and 25 plants at Tanquary Fjord (b). Dashed lines represent least squares fit for each phenological phase..... 53

FIGURE 2.6 Floral budding dynamics (number of buds produced on each plant of *Dryas integrifolia* each year) between 1992-2005 at Baker Lake (a) and between 1994-2005 at Tanquary Fjord (b)..... 54

FIGURE 2.7 Mean number of floral buds from 1992 to 2005 (means ± SE) (a) and percent deviation from mean number of floral buds 1994-2005 (b) in permanently marked plants of *Dryas integrifolia* at Baker Lake (n = 30) and Tanquary (n = 25). 55

FIGURE A1.1 Localisation du site ITEX – « International Tundra Experiment » de Baker Lake, Nunavut (64°10'N, 95°30'W). 65

FIGURE A1.2 Anciennes crêtes de plages du côté nord du lac de Baker Lake, Nunavut (a) et vue vers le sud-ouest à partir du site ITEX (b)..... 66

FIGURE A1.3 Quadrat de 50 cm x 50 cm utilisé sur le site. 67

FIGURE A1.4 Comparaison entre les températures moyennes journalières 68
enregistrées à 1,5 m à la station d'Environnement Canada Baker Lake A et celles enregistrées par senseur HOBO (moyenne journalière des températures prises aux 10 minutes) à 1 cm à l'intérieur du sol sous des plants de *Dryas integrifolia* au site ITEX de Baker Lake durant juillet 2005. Les écarts-types pour chaque période de 24 heures sont présentés par le diagramme à barres. 68

FIGURE A1.5 Omniprésence du lichen *Alectoria* (de couleur noire) autour des plants de *Dryas integrifolia* au site ITEX et dans les environs du site parmi *Empetrum nigrum* et *D. integrifolia.* 71

FIGURE A2.1 Serres ouvertes « Open Top Chambers » (OTC) simulant un réchauffement climatique sur les plants de *Dryas integrifolia* du site ITEX de Baker Lake, 62°N, Nunavut. 74

FIGURE A2.2 Températures moyennes et écarts-types des parcelles réchauffées (OTC) et témoins (CTRL) en Juillet 2005 et comparaison avec variabilité inter-annuelle des températures de surface pour Juillet (1990-2005). 75

CHAPITRE 1

RÉSUMÉ SUBSTANTIEL

1.1 INTRODUCTION

De par la rapidité des changements climatiques qui y sont observés, l'Arctique se situe au cœur du débat sur les réchauffements à l'échelle planétaire (Overpeck *et al.* 1997, Serreze *et al.* 2000, ACIA 2005, IPCC 2007). Conséquemment, on y prévoit des changements de la composition et de la répartition des communautés végétales (ACIA 2005). Cela pourrait provoquer des modifications de la production primaire nette et des cycles biogéochimiques engendrant un impact sur les organismes des niveaux trophiques plus élevés (Eviner et Chapin 2003). De plus, en modifiant l'albedo du sol, la végétation pourrait à son tour contribuer à accentuer le réchauffement en cours (Bliss *et al.* 1973, Shaver *et al.* 2000, Wookey 2002). Comprendre la nature des variations climatiques et leur impact sur la végétation s'avère essentiel pour anticiper l'évolution du biome de la toundra qui occupe 15 % des terres de la planète (Bliss 1971) et qui pourrait être appelé à diminuer de 42 % dans les 50 prochaines années en réponse au réchauffement global (Kaplan et New 2006). Comme ces territoires sont en général peu modifiés par l'homme, les changements globaux s'y manifesteront de façon plus claire que dans les autres biomes (Wookey 2002). L'Arctique est donc tout indiqué pour mesurer l'impact des changements globaux en étudiant, entre autre, leur influence sur l'écologie de la reproduction des plantes et la phénologie (i.e. moment où la croissance, la reproduction, la sénescence sont initiées chaque année).

Des études expérimentales ont démontré que les plantes de la toundra peuvent répondre de façon rapide à des manipulations environnementales (Arft *et al.* 1999, Phoenix et Lee 2004). Une méta-analyse regroupant onze sites d'étude à travers ce biome rapporte qu'en aussi peu que deux années de réchauffement expérimental de l'ordre de 1 °C à 3 °C, une augmentation de la hauteur et du couvert des arbustes décidus et des

graminées de même qu'une diminution de la richesse spécifique ont été observées (Walker *et al.* 2006). Après une décennie de suivi en conditions naturelles, la végétation de type« tussock tundra » des sites bas-arctiques de Toolik Lake en Alaska (Chapin *et al.* 1995, Chapin et Shaver 1996) révélait des changements au niveau des communautés et des formes de croissance dominés par la progression des arbustes ayant amené une diminution des cryptogames (bryophytes et lichens). De façon générale, il a aussi été observé que le réchauffement provoque une plus grande réponse végétative dans le Bas-Arctique tandis qu'une augmentation de l'effort de reproduction est le plus souvent notée dans le Haut-Arctique (Arft *et al.* 1999, Walker *et al.* 2006).

La phénologie des végétaux constitue l'aspect de la nature le plus sensible aux changements climatiques et le plus facile à observer (Sparks & Menzel 2002) d'où son appellation d' « empreinte digitale » des changements climatiques (Parmesan et Yohe 2003). Malgré une saison de croissance très courte dans l'Arctique, il y a une grande variation de la phénologie de floraison entre les espèces (Shaver et Kummerow 1992). Comme la phénologie de floraison affecte le succès de reproduction des plantes qui disposent d'une saison de croissance très courte, cela constitue un élément clé pour comprendre l'écologie de la flore arctique (Thòrhallsdòttir 1998, Molau 1993). Molau (1993) suggère même que la majeure partie de la variation dans les patrons de reproduction des plantes arctiques est reliée à un seul facteur : la phénologie de floraison. En plus d'un effet direct sur le succès reproducteur et la colonisation végétale, la phénologie peut avoir un effet indirect à d'autres niveaux, notamment sur les herbivores et les pollinisateurs (Wookey 2002). Comprendre comment les espèces ont répondu aux températures passées peut aider à prédire comment elles pourraient répondre au réchauffement climatique (Sparks et Menzel 2002).

1.2 PROBLÉMATIQUE

La plupart des travaux existants sur l'impact des réchauffements climatiques sur les plantes de toundra se sont concentrés sur des réponses à court terme des plantes (moins de cinq ans) (Arft *et al.* 1999). Souvent, cette période n'est pas assez longue pour documenter la variabilité naturelle et refléter les impacts des changements climatiques à

plus long terme (Chapin et Shaver 1995, Shaver *et al.* 2000, Dormann et Woodin 2002, Epstien *et al.* 2004). Les données publiées pour ces latitudes proviennent souvent de sites humides de l'Alaska (dominés par des arbustes, des graminées et des mousses) peu comparables avec l'Est de l'Arctique (Territoires du Nord-Ouest et Nunavut continental) où les sols sont encore peu développés, ayant subi la dernière glaciation (Bliss et Matveyeva 1992). Aussi, la plupart des sites d'étude dans l'Arctique étant côtiers, l'immense portion de toundra retrouvée à l'intérieur des terres n'est jusqu'à présent que très peu étudiée. On constate également que, contrairement aux régions tempérées qui disposent de registres phénologiques à long terme (Sparks and Carey 1995, Sparks *et al.* 2000, Menzel 2000, Menzel 2001), ceux-ci sont rares pour les plantes de l'Arctique et que l'on comprend très peu les changements de phase en fin de saison (Wijk *et al.* 2003, Sparks & Menzel, 2002, Lechowicz 1995).

Il existe à notre connaissance seulement deux études à long terme portant sur la phénologie en toundra. Molau *et al.* (2005) ont démontré en milieu subarctique alpin, sur une période de 10 ans, que la séquence de floraison (l'ordre selon lequel une espèce fleurit par rapport aux autres espèces) et le nombre de degrés-jours au dessus de 0°C nécessaires à la floraison de 144 espèces était plutôt constant d'année en année malgré une grande variation inter-annuelle de la première date de floraison de chaque espèce. Ces données soutiennent la classification des plantes selon leur forme de vie (« Life forms ») et le stade auquel leurs bourgeons floraux hivernent de Sorensen (1941) qui permettait déjà de prédire la constance de la relation entre les degrés-jours et la date de floraison des plantes de toundra. Une autre étude à long terme en Islande (Thòrhallsdòttir 1998) comparant, sur un « pool » de 74 espèces, le nombre d'espèces en fleurs à la même date pendant 11 années, indique des liens entre les températures de juin et la phénologie de reproduction. Ces travaux ne font toutefois pas de lien entre la phénologie, l'effort de reproduction et les facteurs environnementaux qui influencent leur variation inter-annuelle.

Bien qu'on sache que l'allocation à la reproduction sexuée varie grandement entre les années et que la variation inter-annuelle de floraison est uniforme sur de grandes régions

en toundra (Shaver et Kummerow 1992), on l'a rarement démontré scientifiquement et les contrôles climatiques dans cette allocation ne sont pas bien compris. Grâce aux travaux de Sorensen (1941), Billing et Mooney (1968), Geber *et al.* (1997) et Diggle (1997), nous savons que plusieurs plantes des milieux froids préforment leurs bourgeons reproductifs durant la ou les saisons précédant la floraison. Pourtant, aucun lien entre les conditions environnementales de la saison précédente et l'effort ou la phénologie de reproduction n'a été trouvé dans l'étude à long terme de Thòrhallsdòttir (1998). Il reste donc à savoir quels sont les facteurs qui influencent l'allocation des ressources au moment de la préformation des bourgeons et laquelle des saisons impliquée dans ce processus a le plus d'influence (*i.e.* combien d'années avant la floraison) (Körner 1999).

De plus, peu d'études incluent les conditions hivernales dans leur analyse de l'influence climatique sur la végétation (Aerts *et al.* 2004). Pourtant c'est durant l'hiver que les modèles de circulation générale prédisent les plus grands changements climatiques dans l'Arctique (Maxwell 1992, IPCC 2007).

Finalement, la littérature rapportant les effets à long terme des variations climatiques sur la végétation du Haut-Arctique est encore quasi-inexistante. Contrairement au milieu subarctique et au Bas-Arctique où des variations climatiques ont entraîné des migrations importantes de la végétation, les changements dans le Haut-Arctique semblent plutôt qualitatifs (ex. : potentiel reproductif, taille des individus) (Svoboda 1974, Arft *et al.* 1999). Les changements planétaires risquent donc d'avoir une dynamique très différente dans le Haut-Arctique et comme il y a peu de compétition pour l'espace, la reproduction sexuée pourrait bien jouer un rôle important dans la colonisation d'espaces ouverts. Comme les réponses aux changements climatiques diffèrent grandement d'une espèce à l'autre (Arft *et al.* 1999, Dormann et Woodin 2002, Wookey 2002), l'étude à l'échelle des espèces circumpolaires (plutôt qu'à l'échelle des communautés ou des types fonctionnels) sur une variété de sites est recommandée (Henry et Molau 1997).

Dans le cadre de la présente étude, nous avons analysé 13 années d'observations détaillées sur la phénologie et l'effort de reproduction de *Dryas integrifolia* Vahl., une

espèce pérenne structurante de la toundra arctique Nord-Américaine et Groenlandaise (Murray 1997). Ces données ont été initiées par Dr. Josef Svoboda (University of Toronto) en 1992 et proviennent de deux sites d'étude situés au Nunavut, dans l'Arctique canadien. Notre recherche s'inscrit dans le programme ITEX (International Tundra Experiment), un réseau circumpolaire de sites alpins et arctiques qui utilisent des protocoles standardisés de mesure de la réponse des espèces et des communautés végétales aux changements climatiques expérimentaux ou observés (Molau et Molgaard 1998). L'hypothèse générale de cette étude est que les variations inter-annuelles du climat sont significativement associées aux variations de la phénologie et de l'effort de reproduction de *D. integrifolia.*

1.3 OBJECTIFS

Notre recherche vise à améliorer la compréhension de la reproduction des plantes arctiques par l'identification des facteurs climatiques qui sont reliés à la variation inter-annuelle de la reproduction de *Dryas integrifolia.* Une meilleure compréhension des dynamiques de phénologie et de reproduction de cette espèce très répandue dans la toundra arctique est susceptible de nous aider à prédire quels effets pourraient avoir les changements planétaires sur ses populations. Comme les hautes latitudes démontrent des variations à l'échelle régionale des changements environnementaux, notamment dans les températures de surface, les précipitations et les conditions du pergélisol (Serreze *et al.* 2000), la première étape de cette étude visait la caractérisation des variations climatiques inter-annuelles des deux sites d'échantillonnage. Cela a permis de déceler les tendances climatiques générales pour la période de l'étude, soit 1990-2005. Les données climatiques ont ensuite été mises en relation avec les paramètres de la végétation et ont permis de répondre aux questions suivantes:

(1) Quelles sont les variables climatiques qui influencent la phénologie et l'effort de reproduction de *D. integrifolia?*
(2) Est-ce que les liens climat-végétation sont différents entre les deux sites séparés par 17° de latitude?

(3) Quelles sont les implications de nos résultats dans le contexte des changements planétaires?

Le chapitre 2 de ce mémoire présente ces résultats sous forme d'article scientifique. En annexe, on retrouve une caractérisation approfondie de la végétation et du sol du site de Baker Lake ainsi que les mesures de micro-météorologie effectuées lors des travaux de terrain menés durant l'été 2005.

1.4 MÉTHODES

Les observations se sont déroulées sur deux sites du Nunavut, dans l'Arctique canadien. Le site de Baker Lake (64°12'N, 95°30'W) constitue le seul site ITEX de l'écozone arctique du Canada situé à l'intérieur des terres (les autres sont côtiers) et bénéficie de données climatologiques à long terme (depuis 1945). Il est caractérisé par un climat continental-arctique et une végétation de toundra avec quelques rares arbustes érigés. Le couvert végétal y est de près de 100 % et *Dryas integrifolia* ainsi que *Empetrum nigrum* sont les espèces vasculaires dominantes. Le site de Tanquary Fjord (81°24'N, 76°52'W), sur l'île d'Ellesmere, fait partie du Parc National de Quttinirpaaq. Le climat y est de type océanique-arctique avec très peu de précipitations et la végétation du site correspond au domaine du désert semi-polaire avec *Saxifraga oppositifolia* L., *Papaver radicatum* Rottb. et *D. integrifolia* parmi les principales plantes à fleurs.

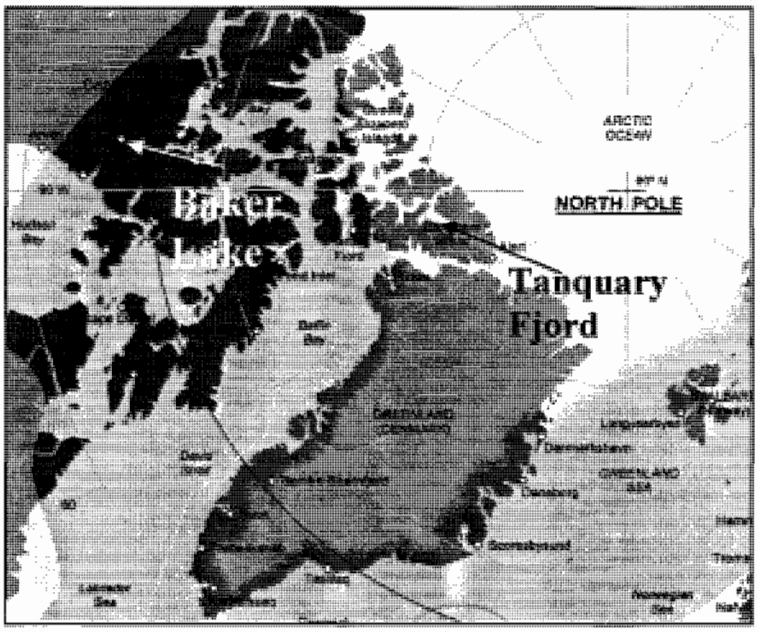

FIGURE 1.1 Localisation des sites d'étude au Nunavut, Canada (Baker Lake (64° N) et Tanquary Fjord sur l'île d'Ellesmere (81° N)).

À Baker Lake, les données de températures et de précipitations proviennent de la station météorologique «Baker Lake A» d'Environnement Canada située à moins d'un kilomètre du site d'étude. À Tanquary Fjord, une station automatisée alimentée par énergie solaire est entretenue par Parcs Canada et se retrouve à quelques mètres du site. Dans les deux cas, les températures sont mesurées à 1,5 m au dessus du sol. Les degrés-jours sans gel ont été calculés par la somme cumulative des degrés au-dessus de zéro à partir des températures moyennes journalières pour les mois de mai à octobre de chaque année. Les totaux pluviométriques journaliers de mai à octobre ont été utilisés pour calculer le nombre de jours avec des précipitations liquides.

Comme nos analyses nécessitaient certaines données non disponibles pour la station de Tanquary Fjord (normales saisonnières des températures pour la période 1971-2000 et totaux pluviométriques estivaux), nous avons dû utiliser des données provenant de la station d'Environnement Canada « Eureka » située également sur l'île d'Ellesmere. Cette station, bien que située à plus de 200 km du site de Tanquary, est la station la plus proche fournissant des données à long terme permettant le calcul des anomalies climatiques par rapport aux normales pour 1971-2000.

Durant les travaux de terrain menés au site de Baker Lake (été 2005), des mesures de micro-météorologie ont été prises à l'aide de « datalogger » HOBO (H8). Vingt senseurs ont été placés à 1 cm de la surface du sol, sous différentes plantes vasculaires, sous une couverture de lichen du genre *Alectoria* et sous des surfaces de sol nu.

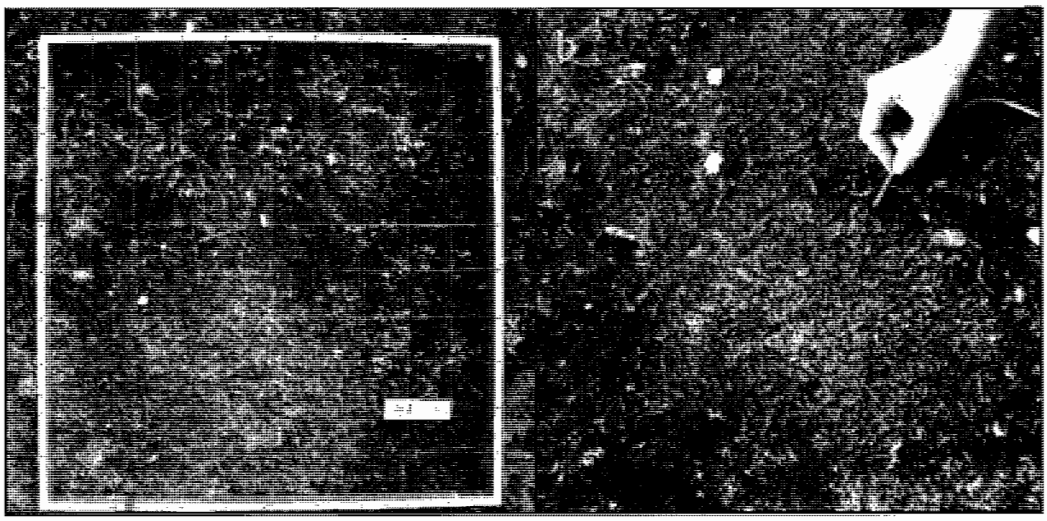

FIGURE 1.2 a) Quadrat de 50 cm x 50 cm utilisé pour la caractérisation de la végétation à Baker Lake, Nunavut. b) Senseur HOBO placé sous un plant de *Dryas integrifolia.*

La température était enregistrée aux dix minutes entre le 4 juillet et le 2 août 2005. Une caractérisation de la végétation et du sol du site a aussi été effectuée à l'aide de 30 quadrats de 50 cm x 50 cm qui ont été disposés de façon aléatoire sur le site. Le pourcentage de recouvrement par espèce pour les plantes vasculaires et par genre pour les invasculaires était noté pour chaque quadrat et la moyenne des données provenant des quadrats donnait un portrait global du site. Cinq échantillons de sol furent prélevés au site, tamisés (2 mm) et pesés pour en analyser le contenu en carbone, azote, phosphore et potassium ainsi que le pH et la texture.

L'espèce étudiée, *Dryas integrifolia,* est un arbuste nain sempervirent occupant de grandes proportions de la toundra arctique et alpine, surtout les terrains nus et les substrats rocheux (Porsild 1955). Les akènes immatures de *D. integrifolia* sont une

source de nourriture pour plusieurs espèces de petits rongeurs, d'oiseaux et le bœuf musqué (Aiken 2002).

Les suivis phénologiques de 1992 à 2005 à Baker Lake et de 1994 à 2005 à Tanquary Fjord ont été effectués selon le protocole établi par le programme « International Tundra Experiment » (ITEX; Molau et Molgaard 1998). Ce design expérimental utilise des mesures répétées où les mêmes individus sont suivis au fil des années. Trente plantes de *D. integrifolia* ont été marquées à Baker Lake et vingt-cinq à Tanquary Fjord. Les sites ont été visités à tous les 3 jours durant la saison de croissance, soit approximativement entre le 15 juin et le 15 août de chaque année. La date d'occurrence des stades phénologiques de la reproduction (bourgeonnement, floraison, fanaison, fructification (akènes), dispersion des akènes) de chaque plant a été enregistrée en jours de l'année. Les mesures telles que le nombre de bourgeons, le nombre de fleurs, le nombre de fleurs transformées en fruit et la taille des pédoncules floraux ont aussi été enregistrées pour chaque individu à chaque visite et nous ont permis de quantifier l'effort de reproduction total pour chaque saison de croissance.

FIGURE 1.3 a) *Dryas integrifolia*, une espèce structurante de la toundra. Photo prise près du site d'étude de Baker Lake, Nunavut. b) Akènes de *D. integrifolia.*

Les tendances climatiques pour les stations de Baker Lake et Tanquary Fjord ont été analysées par calcul des anomalies (valeurs centrées et réduites) saisonnières des températures de surface et des précipitations par rapport aux normales respectives pour la période de 1971-2000. Un filtre non récursif passe-bas de Hanning d'ordre 2 (moyennes mobiles pondérées) a aussi été appliqué aux anomalies pour dégager une tendance plus générale pour la période 1990-2005 (Assani 1999). Nous avons aussi quantifié les variations inter-annuelles de températures à nos deux sites pour la période de l'étude (1990-2005). Les relations entre les facteurs environnementaux et l'effort de reproduction et la phénologie ont été testées à l'aide de régressions multiples. Les données climatiques (voir Tableaux 2.2 et 2.3, Chapitre 2 pour la liste complète des variables) associées à chaque saison de croissance de même que les conditions des deux saisons précédentes (ex : degrés-jours de l'été précédent, degrés-jours de l'été il y a deux ans) ont été utilisées comme variables indépendantes. Nous avons procédé aux régressions multiples par la méthode « stepwise forward » qui intègre une variable à la fois dans le modèle par ordre décroissant de son influence. Comme il y avait une autocorrélation temporelle des résidus, les modèles ont été transformés selon la méthode Yule-Walker (SAS Institute Inc. 1999). Toutes les analyses statistiques ont été effectuées à l'aide de SAS/STAT software (version 2005).

1.5 RÉSULTATS

Durant la période de notre étude, les températures de surface ont été, en majorité, au-dessus des normales de 1971-2000 aux deux sites. Les variations inter-annuelles des températures moyennes ont été les plus grandes durant l'automne et l'hiver à Tanquary et le printemps et l'automne à Baker Lake mais les degrés-jours sans gel accumulés durant l'été variaient aussi énormément (de 626 à 1220 à Baker Lake et 285 à 671 à Tanquary). Les totaux pluviométriques montraient également une grande variabilité inter-annuelle et à Eureka, en 1997 et 2002, ces totaux se situaient respectivement à 57 % et 72 % au-dessus des normales pour 1971-2000.

L'espèce étudiée montrait une forte association aux variations climatiques. Les dates de bourgeonnement et de floraison de *Dryas integrifolia* variaient d'année en année sur près de 20 jours durant la période de 1992-2005 et le moment de la floraison était principalement relié à la date de fonte des neiges à Baker Lake et au nombre de degrés-jours sans gel accumulés en juin à Tanquary. Pour la période de notre étude, une tendance vers une floraison plus hâtive de *D. integrifolia* est apparente au site de Tanquary. En effet, la floraison s'y est graduellement avancée de plus de 10 jours entre 1994 et 2005. Par contre, au site de Baker Lake, seule une grande variabilité inter-annuelle est apparente.

Le nombre de degrés-jours entre le stade de bourgeonnement et celui de fructification était relativement constant d'année en année. La fructification était atteinte en moyenne après 366 ± 24 degrés-jours sans gel. Cela indique que durant un été plus froid que la moyenne, *D. integrifolia* n'arrive probablement pas à compléter la maturation de ses graines. Un réchauffement climatique risque donc d'avantager *Dryas* dans le Haut-Arctique, où les saisons de croissance n'accumulent pas toujours le nombre minimal de degrés-jours nécessaires au succès de reproduction.

Le nombre de bourgeons et de fleurs produites par plante variait inter-annuellement de façon synchrone entre les plantes d'un même site et dans une certaine mesure, entre les deux populations étudiées, bien qu'elles soient séparées par 17 degrés de latitude. Les facteurs influençant la variabilité de l'effort de reproduction sont toutefois différents aux deux sites. À Baker Lake, un été chaud deux ans avant la floraison, suivi d'un été pluvieux l'année précédente et ensuite d'un mois de juin frais semblent fournir la séquence menant à une forte floraison pour *D. integrifolia*. Pour les plantes de Tanquary, plus il y a de chaleur durant le mois d'août de l'été précédent la floraison, plus les bourgeons floraux seront nombreux.

Les observations effectuées au site ITEX de Baker Lake en 2005 indiquent que les températures de surface enregistrées par la station d'Environnement Canada sont légèrement inférieures à celles mesurées à l'intérieur des plantes de *D. integrifolia*, et ce,

surtout durant les jours ensoleillés. De plus, l'écart journalier des températures tend à être plus grand au niveau du sol qu'à 1,5 m. Ce site présente une faible diversité d'espèces vasculaires et leur recouvrement total n'est que de 41 %. Le lichen du genre *Alectoria* est le plus répandu à ce site. Nos analyses indiquent aussi que le site possède un sol acide et très drainant avec un très faible pourcentage d'azote.

1.6 CONCLUSIONS

La présente recherche démontre le lien étroit entre les variables environnementales et la dynamique de reproduction de *Dryas integrifolia*. Une combinaison de conditions climatiques de plus d'une saison sont reliées à l'effort de reproduction de cette plante à longue vie et bien qu'un réchauffement climatique puisse contribuer à une plus grande production de bourgeons floraux préformés, à une période plus longue de stockage des réserves à l'automne et à une meilleure maturation des graines, on constate aussi que trop de chaleur en juin pourrait nuire à la floraison de *D. integrifolia*. La plasticité phénologique de l'espèce, comme l'indique nos résultats, porte à croire qu'elle pourrait agir comme baromètre des changements climatiques. Davantage d'études à long terme dans le Haut-Arctique seront nécessaires pour prédire dans quelle mesure d'autres espèces de ce type (plantes pérennes dominantes de la toundra à floraison hâtive ou de mi-saison) réagissent de la même façon que *D. integrifolia* aux variations climatiques.

CHAPITRE 2

PHENOLOGY, REPRODUCTIVE EFFORT AND CLIMATE VARIABILITY: A 13-YEAR STUDY IN THE CANADIAN ARCTIC

Lucie-Guylaine Levasseur and Esther Lévesque

2.1 RÉSUMÉ

Les registres à long terme de la phénologie et de la dynamique de reproduction de la végétation en relation avec la variabilité climatique sont peu nombreux dans l'Arctique, surtout pour le Haut-Arctique. Cet article présente les résultats de 13 années d'observations détaillées de la phénologie et de l'effort de reproduction de *Dryas integrifolia* Vahl., une espèce vasculaire structurante de la toundra Nord-Américaine et Groenlandaise. Nos données proviennent du site bas arctique de Baker Lake (64°N) et du site haut arctique de Tanquary Fjord (81°N). Tous deux sont situés au Nunavut, Canada et font partie du réseau circumpolaire ITEX (International Tundra Experiment). Notre but était de caractériser la variabilité climatique des deux sites et de la mettre en relation avec les variations inter-annuelles de phénologie et d'effort de reproduction de *D. integrifolia*. Durant la période de l'étude (1990-2005), les degrés-jours sans gel et les totaux pluviométriques estivaux démontraient une grande variabilité inter-annuelle. De plus, les moyennes saisonnières et annuelles des températures de surface se situaient, de façon générale, bien au-dessus des normales pour la période 1971-2000. *Dryas integrifolia* démontrait une forte association phénologique à la variabilité climatique. Entre 1992 et 2005, le jour moyen de bourgeonnement variait inter-annuellement sur plus de 20 jours aux deux sites. Le principal facteur associé au moment de la floraison était la date de fonte des neiges à Baker Lake et la chaleur accumulée en juin à Tanquary. La floraison de *D. integrifolia* s'est graduellement avancée de plus de 10 jours entre 1994 et 2005 au site de Tanquary. Le nombre de degrés-jours entre le stade de bourgeonnement et celui de fructification était relativement constant d'année en année aux deux sites. À Baker Lake, un été chaud deux ans avant la floraison, suivi d'un été pluvieux l'année précédente et ensuite d'un mois de juin frais semblait être la séquence menant à une forte floraison pour *D. integrifolia*. Pour les plantes de Tanquary, plus il y avait de chaleur durant le mois d'août de l'été précédent la floraison, plus les bourgeons floraux étaient nombreux. Le nombre de bourgeons et de fleurs produites par plante variait inter-annuellement de façon synchrone entre les plantes d'un même site et dans une certaine mesure, entre les deux sites, indiquant que les patrons climatiques à large échelle spatiale ont le potentiel d'influencer la dynamique de reproduction sur de grandes régions.

2.2 ABSTRACT

Long-term records of plant phenology and reproduction dynamics in relation with climate variability are sparse in the Arctic and rare in the High Arctic. We are presenting here the results of 13 years of detailed observations of the phenology and reproductive effort of *Dryas integrifolia* Vahl., a dominant vascular plant species over wide areas of the North American and Greenland tundra biome. Our data come from the low arctic site Baker Lake (64°N) and the high arctic site Tanquary Fjord (81°N), both located in Nunavut, Canada. These sites are part of the ITEX (International Tundra Experiment) network, a circumpolar effort to assess the impact of climate change on tundra plant populations and communities. Our goal was to caracterise the climate variability of the two sites and to identify the climatic factors that are associated with the phenology (timing of budding, flowering and fruiting) and the interannual variation of reproductive effort of *D. integrifolia*. During the study period (1990-2005), there was a great variation in thawing degree-days and liquid precipitation totals accumulated annually at both sites. In addition, the seasonal and annual mean surface temperatures were generally well above the 1971-2000 normals. Our results suggest that *D.integrifolia* is showing a strong phenological response to climate variability. Onset of budding varied over a nearly 20 days range between 1992 and 2005 at both sites. At Tanquary (high arctic site), the *Dryas* population gradually advanced its flowering date by more than 10 days since 1994. The amount of degree-days from the bud to the fruit stage was rather constant among years. While the onset of flowering was triggered by snowmelt at Baker Lake, accumulated heat in June was the main influencial factor at Tanquary. Interannual variations of *Dryas* reproductive effort were important and correlated with different climatic factors at the two sites. At Baker Lake, a cool spring prior to bud burst as well as a rainy summer the previous year and a warm summer two years before were all significantly linked to a higher number of buds and flowers produced. At Tanquary, only the heat accumulated in August of the previous summer had an association (positive) with the number of flowers produced. Interannual variations of reproductive effort were synchronous among plants of a site and to some extent, between populations of the two sites separated by 17 degrees of latitude. This

indicates that large scale climatic patterns have the potential to modify the reproduction dynamics of this tundra plant over wide regions.

2.3 INTRODUCTION

Global Circulation Models (GCM) are not only predicting that warming will be more severe at high latitudes (4 °C increase by 2080) but also forecast an increased variability of temperatures and precipitations in the Arctic (ACIA 2005). While many studies simulating the effect of climate warming on vegetation have been conducted in the tundra biome during the last two decades (Wookey *et al.* 1993, Chapin *et al.* 1995, Henry and Molau 1997, Sandvik *et al.* 2004, Wahren *et al.* 2005, Hollister *et al.* 2005), we still know very little about the impact of interannual climatic variations on tundra plants. Long term studies assessing these impacts are rare for the Arctic, especially for High Arctic plant communities.

One aspect of nature that responds quickly to climate variations is phenology (Sparks and Menzel 2002, Parmesan and Yohe 2003, Walther 2003) which is the study of the timing of recurring biological events (*e.g.*: growth, reproduction, senescence and dormance) and their biotic and abiotic causes (Leith 1974). Plant phenology has a large impact on interannual variation of gross primary production (GPP) and on carbon dioxide uptake (Welker *et al.* 1997). According to Wijk *et al.* (2003) a difference of 6 days at the start of the growing season could result in differences of more than 10 % in annual GPP. Moreover, the quick phenological response of plants to climate warming could change the relationships that they have with pollinators, seed dispersers, herbivores, seed predators and pathogens (Dunne *et al.* 2003). Even though the growing season is very short in arctic tundra, large variations in flowering phenology occur among species (Shaver and Kummerow 1992) and from year to year, which influence reproduction success (Thòrhallsdòttir 1998, Molau 1993). Despite their ecological importance, phenological records are almost non existant in the Arctic. To our knowledge, there has been only two long term studies on plant phenology in the tundra biome. In an 11 years study, Thòrhallsdòttir (1998), compared the proportion of species in flower at the same date every year and found that June temperature influenced the time of flowering. A 10 years study by Molau *et al.* (2005) monitoring the first

flowering dates of 144 species in a subarctic-alpine area showed that temporal sequences of flowering among species and accumulated thawing degree days at first flowering date (FFD) were very constant among years for most species despite large interannual variation of the FFD for each species. They also observed that accumulated thawing degree days and snowmelt date were the main environnemental controls on phenology. Although these studies were conducted on a large variety of species, they monitored only one phenophase and did not consider relations between phenology and reproductive effort and success.

Reproductive dynamics of tundra plants is another biological aspect influenced by climatic variations. Wookey *et al.* (1995) showed that induced experimental warming resulted in an increase seed weight of *Dryas octopetala* L. in alpine and high arctic sites. In an alpine tundra site, Stenström *et al.* (1998) found that accumulated global radiation was the main determinant of interannual variation of reproductive effort of *Saxifraga oppositifolia* L. and other truly evergreen with long-lived leaves like *Diapensia lapponica* and *Cassiope tetragona.* However, environnmental factors acting on variations of reproductive effort of semi-evergreen plants like *Dryas integrifolia* and most tundra plants are still poorly understood. It is important to study the impact of environnemental factors on plant reproduction as large unvegetetad areas in the High Arctic offer opportunity for colonisation by sexual reproduction. While a meta-analysis reported that plant responses to warming were rather vegetative in the Low Arctic and that an increase in reproductive effort was noted in many species in the High Arctic (Arft *et al.* 1999), the lack of long term data from these high latitudes does not allow to corroborate these findings. A recent meta-analysis reporting the results of warming experiments in a variety of sites also observed that changes in cover were not necessarly caused by dominant species and fewer species tended to produce a larger proportion of the cover in response to warming (Walker *et al.* 2006). Studying today's dominant species' reproductive ecology might give us insights on their limitations to colonise empty spaces and maintain there presence in a plant community in the future.

In this paper we examine the impact of interannual climatic variations on plant phenology and reproductive effort. We are using 13 years of detailed observations of reproductive effort and dates of budding, flowering and fruiting of *D. integrifolia*, a dominant vascular plant over vast areas of arctic and alpine tundra. These data come from populations of *D. integrifolia* at two sites of the canadian Arctic that are part of the worldwide International Tunda Experiment (ITEX), a network of tundra sites where vegetation responses to predicted climate warming is studied (Henry and Molau 1997, Arft *et al.* 1999). The aims of our study were (1) to identify the climatic factors that are associated with interannual variations of phenology and reproductive effort of *D. integrifolia*, (2) to verify if these climate-vegetation relations are different between low and high arctic sites and (3) to assess the implications of our results in the context of global change.

2.4 MATERIALS AND METHODS

2.4.1 Research Sites

The two sites are species-poor fellfields situated in Nunavut Territory, Canada, but are subjected to different temperature and precipitation regimes (Table 2.1).

Baker Lake (64°10'N, 95°30'W) (Figure 2.1), is located at the northern limit of the low arctic ecoclimate zone, near the Inuit community and lake of the same name, which are roughly 125 km inland from the northwest shore of the Hudson Bay, making it the only interior site among the ITEX arctic sites. Vegetation of this arctic subzone is classified as Erected Dwarf Shrub Tundra on the Circumpolar Arctic Vegetation Map (CAVM Team 2003). At the study site, *Dryas integrifolia* Vahl. grows on an exposed ridge of the Canadian Shield which has acidic soils and high drainage. Average annual temperature at Baker Lake is –11.3 °C with mean July temperature reaching 11.4 °C.

Tanquary Fjord (81°24'N, 76°52'W) (Figure 2.1), is located on Ellesmere Island, within Quttinirpaaq National Park. It experiences a high arctic ecoclimate with low precipitations (33 mm of rain and 40 cm of snow yearly) and low annual mean temperatures (-17 °C), mean temperature of the warmest month (July) being only 7 °C. It is botanically classified as a polar semi-desert (Bliss 1977) or a Prostrate Dwarf Shrubs Tundra (CAVM Team 2003). Water limitation and coarse surface rock debris limit the distribution and abundance of plants (Bean and Henry 2002). The two vegetation zones represented by our sites compose the majority (64 %) of the Canadian Arctic (Walker *et al.* 2005).

2.4.2 Study Species

Dryas integrifolia Vahl. (Rosaceae) is a long-lived evergreen dwarf shrub widespread in the Canadian Arctic and Greenland tundra and it is the most characteristic and dominant species of the southern polar semi-deserts (Svoboda 1977). Along with the closely

related *Dryas octopetala* L., these mat forming shrubs provide the dominant plant cover for large expanses of circumpolar and alpine tundra (Murray 1997). *Dryas integrifolia* is a pioneer species found in a wide range of habitats and substrates with a preference for mesic to dry soils with low organic content (Aiken *et al.* 1999). Althought *D. integrifolia* is classified as a calciphilous species (Cody 2000), it grows profusely on acid granitic soils in Baker Lake, Nunavut, one of our study sites (see *Research sites* section). The *Dryas* genus is known to be associated with mycorrhizal fungus (Melville *et al.* 1987, Lawrence *et al.* 1967) and to be nitrogen fixer (Lawrence *et al.*1967). However, in a study conducted in a polar semi-desert on Devon Island, Canada, *D. integrifolia* plants sampled did not show nitrogen fixing nodules (Stutz and Bliss 1975).

Floral buds of *D. integrifolia* are pre-formed the year preceding emergence (Sorensen 1941) and reproductive effort shows significant interannual variability (Welker *et al.* 1997). Reproductive phenology and seed weight and viability of *D. octopetala* respond to experimental warming (Wookey *et al.* 1993, 1995). The *Dryas* genus is undoubtedly showing responses to both observed and experimental climate warming but environmental factors influencing the interannual variability of phenology and reproductive effort are still unclear. Published long term studies on *D. integrifolia* reproductive dynamics in arctic ecosystems are inexistant.

2.4.3 Climatic data

Temperature and precipitation data for Baker Lake site were recorded at the Environment Canada standard meteorological station "Baker Lake A" located 1.7 km from the study site (Environment Canada 2005). At Tanquary Fjord site, daily temperatures data from an on-site automatic microclimate station maintained by Parks Canada were used. Precipitation data from the Environment Canada Station "Eureka", the closest long term climate station, were used to represent Tanquary site. Missing temperature data in the spring and summer months for the period 1990-2005 were estimated with a linear regression between Eureka and Tanquary daily temperatures using the same month from the preceding and the following year, Tanquary site being

generally a little warmer than Eureka. In the winter, the temperature relations between Tanquary and Eureka stations were non linear, so any missing data for the cold season was not considered in the analysis.

At both sites, liquid precipitation frequency (rain days or wet days) was assessed by cumulating number of days where the Environment Canada stations reported at least traces of rain. Because most precipitation events do not generate measurable amounts of water and some water is deposited as fog and mist in the Arctic (Woo & Steer 1979), cumulating days with at least traces of rain represents the closest measure of days that had a potential of depositing humidity on the plants. For both sites, mean, maximum and minimum daily temperatures measured 1.5 m above ground were used to calculate annual and monthly thawing degree days (cumulative sum of degrees above 0 °C), and number of days with temperatures above 0 °C. At Baker Lake, an additional derived variable, Freezing Degree Days (FDD), was also used in the analysis and represented the cumulative sum of degrees below -10 °C before 10 cm of snow has accumulated on the ground (calculated from the minimum daily temperatures in fall/winter). FDD was used to assess if there was damage on floral buds from cold temperatures when snow protection was insufficient as arctic plants do not have protective scales on their floral buds (Savile 1972).

2.4.4 Phenology and flower production

Phenology and reproductive effort monitoring was initiated in 1992 at Baker Lake site (64°N) by Josef Svoboda of the University of Toronto who marked 30 plants of *Dryas integrifolia*. In 1994, he also tagged 25 plants of *D. integrifolia* at Tanquary Fjord site (81°N). Markings consisted of aluminium tags secured by iron wire to the base of the main stem and popsicle sticks around each plant. At Baker Lake, every summer between 1992-2005 (except in 2002), the same plants were monitored every 2 or 3 days generally from the snowmelt date and for a period varying from 10 to 40 days. At Tanquary site, monitoring occurred every summer between 1994 and 2005, throuhgout the whole growing season, every 3 to 4 days. At both sites, number of floral buds, open

flowers, wilted flowers and fruits (twisted achenes and untwisted achenes stages) were recorded at each visit. It was then possible to assess the first, median and last occurrence of each phenophase and to determine total number of buds, flowers and fruits per season for each plant. The number of fruits that produce mature seeds has not been measured every year for logistical reasons (not possible to be in the field late enough in the season). Plants were also photographed 4 times during the study period to assess surface and flower production per surface. At Baker Lake, floral peduncle length was also recorded as a measure of reproductive effort as it has been reported in the study of Welker et al. (1997) that the length of the pedicel was significantly correlated to the number of seeds produced by the closely related *Dryas octopetala.*

2.4.5 Statistical analysis

Surface temperature and precipitation anomalies were determined using centered and reduced means (y(t)=(x(t)-m)/s) where m and s are the mean and standard deviation of the 1971-2000 series (Environment Canada 1971-2000). In addition, a Hanning low-pass filter type 2 was applied to those anomalies to show main periods of excedent and deficit for the study period (Assani 1999).

Multiple regression analyses were performed to assess the meteorological variables associated with phenology and reproductive effort (SAS/STAT 2005). Variables used are presented on Tables 2.2 and 2.3 and were entered into the models by forward selection. To check for collinearity between predictor variables, we used graphic observation of the scatterplots and checked tolerance values for each multiple regression. According to Quinn and Keough (2003) tolerance level of more than 0.1 is acceptable. In our analysis, tolerance values were always higher than 0.8 indicating no collinearity problems of the independent variables. Serial autocorrelation of the residuals was detected by graphic observation of residuals against years and confirmed with a Durbin-Watson test (Quinn and Keough 2003). Corrections for autocorrelation were made by transforming models with the Yule-Walker method (SAS Institute Inc. 1999) using SAS/STAT software (2005).

2.5 RESULTS

2.5.1 Climate

Surface temperature and precipitation anomalies for the study period. Annual and seasonal temperature anomalies (centered and reduced means) evaluated with respect to 1971-2000 means (Figure 2.2) show that the study period (1990-2005) has been, for the most part, warmer than normal at both sites in all seasons. At Eureka Station, the closest long term station to Tanquary Fjord site, annual centered and reduced mean temperatures were more than 1 °C above the 1971-2000 normal for 6 of the 15 years of the study period. Positive anomalies were also recorded in the winter temperatures from 2001 to 2005 with the warmest winter in 2003. Summer seasons showed less severe warming than fall and winter in Eureka except in 2005 which represented the warmest summer of the whole study period. At Baker Lake, filtered data show that the beginning of the study period presented a small temperature deficit as well as the year 2004 which was colder than normal in all seasons (Figure 2.2). Despite those cold episodes, Baker Lake data showed positive anomalies of annual mean temperatures for 11 out of the 15 years of the study, with extreme excedents mainly in the spring and in the fall. Both weather stations representing our sites recorded the warmest fall of the 1990-2005 period in 1998 (Figure 2.2).

During the study period, Eureka station recorded generally higher pluviometric totals than 1971-2000 normals with extreme excedents in 1997 and 2002 (respectively 57 % and 72 % higher than 1971-2000 normals) (Figure 2.3b). Baker Lake data show that precipitations vary interannually without a clear trend towards an increase or decrease in the total amount of liquid precipitations between 1990 and 2005 (Figure 2.3a).

Year to year variability. Both sites showed large interannual variations in their mean surface temperatures (Table 2.4). At Tanquary, this variability was most important between consecutive winters and falls with median interannual variations of respectively 2.89 and 1.76 °C. Two consecutive winters (1994 and 1995) in Tanquary had as much as

9 °C difference in their mean temperatures (december, january, february). At Baker Lake, spring and fall proved to be the most variable seasons with respectively 1.88 and 2.19 °C of median year to year variations. Precipitation patterns showed very high year to year variability at both Baker Lake and Eureka weather stations (Figure 2.3).

Derived climate variables. The average mean thawing degree days (TDD) accumulated at Baker Lake was almost double of those accumulated at Tanquary (Table 2.1). Also, at both sites, there was a two-fold difference between TDD accumulated during the coldest and the warmest summer of the study period. While more than half of the heat was received in July at Tanquary, a common feature of other high arctic sites (Lévesque *et al.* 1997), heat accumulated in July represented only 30 % of total degree days at Baker Lake.

Mean thawing degree-days (TDD) and total number of days with mean temperatures above zero were very low during the 1992 growing season at both sites (Figure 2.4) due to the radiative climate forcing brought about by the late 1991 Mt. Pinatubo eruption (Minnis *et al.* 1993). However, Tanquary site's meteorololgical station recorded an even colder season in 1996 with a total mean thawing degree days of only 285.5 while in Baker Lake, that same summer was the warmest of the whole period 1990-2005 (Figure 2.4a) thus showing the sometimes regional character of climate variability in the Arctic.

In 2000, both sites experienced a growing season almost as short as 1992 with only 103 days above the freezing mark at Baker Lake and 81 days at Tanquary, despite their near average total thawing degree days of 954.3 and 503.8 respectively (Figure 2.4b).

Snowmelt dates were similar at Baker Lake and Eureka station being June 16^{th} ± 11 days and June 9^{th} ± 6 days respectively (mean and standard deviation for 1990-2005). The earlier snowmelt at Eureka station, despite a colder spring than Baker Lake, can be explained by a shallow snow cover, rarely exceeding 20 cm in April whereas snow on the ground varies between 30 and 80 cm in April at Baker Lake station. Date in the fall

with at least 10 cm of snow accumulated on the ground varied more than the snowmelt date: November 5th ± 18 days in Baker Lake and November 2nd ± 33 days in Tanquary (mean and standard deviation). Despite these similitudes in snow free period, the total number of days above freezing was lower at Tanquary than Baker Lake.

2.5.2 Phenological responses

Interannual variability. Very variable, the date of peak budding of *Dryas integrifolia* differed by up to nearly 20 days among years (1992-2005) at both sites. Peak flowering was also variable occuring between June 24th and July 13th at Baker Lake and between June 26th and July 12th at Tanquary. In our study, the peak date of a phenological stage reflects the date at which more than 50 % of the total number of buds or flowers were apparent on a plant. Note that in this paper, the term "budding" always refers to floral buds as we did not monitor vegetative development. First and peak budding dates were highly correlated ($r^2 = 0.933$, $p < 0.0001$, $n = 21$) as well as first and peak flowering dates ($r^2 = 0.9$, $p < 0.0001$, $n = 25$), a relationship previously observed in other arctic species (Molau *et al.* 2005). In our phenological analysis, we are using dates of peak budding and flowering because first appearance of buds or flowers of some plants were missed some years depending on the time of arrival in the field. For the fruiting (twisted achenes) and seed dispersal (untwisted achenes) stages, only dates of first occurrence for each plant were available most years and the mean first date was therefore used in the analysis.

Between sites variability. On average, budding was earlier at Tanquary than at Baker Lake but fruiting stage was reached later at Tanquary. At Baker Lake, 16 ± 4 days separated budding and fruiting stages, whereas 21 ± 7 days separated those two stages in Tanquary, indicating that *Dryas* needs more time at its northern limit and under colder climate to accumulate the degree days necessary to complete reproduction. First date of appearance of fruit could not be predicted by the date of first or peak appearance of the floral bud but thawing degree-days (TDD) accumulated at peak budding date were a good predictor of accumulated TDD necessary for the first fruit ($p = 0.017$ Baker Lake

and p = 0.004 Tanquary) suggesting that the amount of degree-days necessary to bring a bud to the fruit stage was rather constant among years. At Baker Lake, 134 ± 27 thawing degree days (TDD) were required for peak budding, 199 ± 33 for peak flowering and 261 ± 42 for first fruiting (mean and standard deviation for 1992-2005). At Tanquary, less TDD were required for each phenophase (respectively 103 ± 44, 162 ± 42 and 248 ± 42) possibly because less degree days were used to melt the thinner snowcover in the spring making the heat immediately available for the plant.

The moment at which first mature achenes unfurled to be released was only recorded at Baker Lake site during 4 summers. It indicates that *D. integrifolia* requires 366 ± 24 TDD or 23 ± 4 days from budding to complete its reproductive cycle at this site. Climate analysis show that TDD accumulated in a growing season were always superior to that amount at Baker Lake but at Tanquary site, TDD recorded in 1992 and 1996 were really low: 314 and 285 respectively (Figure 2.4). During the exceptionnally cold summer of 1996 at Tanquary, most plants flowered only around July 13th and none of the plants had reached the fruit stage (twisted achenes) on August 10 when mean temperatures were already around the freezing point. Thus, it is very likely that no viable seeds were produced by *D. integrifolia* at Tanquary in 1996. When a growing season is colder than normal or if the snow cover persists longer than usual, the *Dryas* populations of the High Arctic are at risk of not completing sexual reproduction. However, for the length of our study, a simple regression shows that earlier flowering did not result into a higher percentage of buds reaching the fruiting stage, meaning that *D. integrifolia* generally disposes of enough time to complete the relatively short development (23 ± 4 days in Baker Lake) of its preformed floral buds.

Length of phenophases. The mean time span for budding and flowering (mean number of days between first and last bud or first and last flower) also varied interannually at each site. On average, budding was taking place during 6 to 10 days at Baker Lake and 6 to 16 days at Tanquary and mean flowering span from 4 to 11 days at Baker Lake and from 2 to 11 days at Tanquary. However, the length of these periods was not correlated to the total numbers of buds or flowers produced annually which means that during

years of high reproductive effort, floral buds and flowers were not initiated on a longer period than during years of low production. Also, within the same year, plants producing more buds and flowers did not necessarly initiate buds and flowers on a longer period than plants that had fewer. (Plants producing only one or no flower were not included in the analysis). In general, flowers were opening 6 to 8 days after the floral bud appeared. When a plant started to flower, very few new buds were formed, the last bud appearing no more than 2 days after flowering started.

Long-term trends. When comparing the annual dates of peak appearance of buds and flowers and first appearance of fruits of *D. integrifolia* (30 plants in Baker Lake and 25 in Tanquary), a tendancy towards an earlier growing season was clearly demonstrated at Tanquary site for the three phenological phases studied (Figure 2.5b) (peak appearance of buds and flowers and first appearance of fruits). According to our dataset, Tanquary *Dryas* population gradually advanced its flowering date by more than 10 days since 1994. We are also observing that dates of phenological events at Tanquary vary less on a year to year basis than at Baker Lake even if the range of variation for the whole period is similar (Figure 2.5).

Factors associated with phenology. Multiple regressions were performed to find the climatic variables that were most efficient for predicting timing of flowering and fruiting at both sites for *D. integrifolia* (description of the independent variables in Table 2.2). At Baker Lake, thawing degree days accumulated in May and date of snowmelt could together explain 84 % of the variation of date of median flowering date (Table 2.5). At Tanquary, thawing degree days of June explained 51 % of the interannual variation of median flowering date (Table 2.6). The median date of fruiting of Baker Lake plants could be predicted at 43 % by TDD accumulated in June (Table 2.7) whereas Tanquary data did not show any relation between fruiting phenology and climatic variables used in our analysis. Contrary to the findings of Henry and Bean (2002), no relationship was found between phenology and the thawing degree days of the previous season.

Date of budding or flowering event was not correlated with reproductive effort. In fact, none of the phenological variables (date of budding, flowering and fruiting) seem to be correlated to any reproductive effort variables (total number of buds, flowers and fruits, length of floral peduncle).

2.5.3 Reproductive effort

For the study period, the mean number of flower buds per 100 cm^2 was slightly higher at the high arctic site (2.18 ± 1.10) than at the low arctic site (1.65 ± 0.93) (mean ± SE). Mean percentages of buds that reached flowering stage were similar at Baker Lake and Tanquary, 89 and 85 % respectively, and proportions of buds reaching fruit stage were also similar yet variable at both sites: 69 ± 22 % at Baker Lake and 66 ± 15 % at Tanquary (mean ± SD).

Contrary to the findings of Welker *et al.* (1997) for *Dryas octopetala*, floral peduncle length (usually linked with larger, heavier and more viable seeds) was not correlated to a longer growing season or to an earlier snowmelt for *Dryas integrifolia*. Pedicels were on average longer in seasons of high flower production. Floral buds with very short peduncles seem to abort early in the season with the floral bud never opening. Average flowering shoot length varied from 40 to 63 mm among years.

Synchrony within a site. The synchrony coefficient S (Herrera 1998) used to assess the level of synchrony in interannual variation of flowering effort among plants of each site was positive but low (0.21 ± 0.05) in comparison with synchrony coefficient of highly masting species like alpine herb *Chionocloa pallens* that can reach 0.77 (Rees at al. 2002). However, this can be because some plants were producing very little flowers and showed a fairly constant low production from year to year and therefore a low variability. Floral budding dynamics curves for each of the 30 plants in Baker Lake and 25 plants in Tanquary (Figure 2.6) show that years of high flower bud production were fairly synchronous among most plants at each site. *Dryas integrifolia* should not be considered a strict masting species, because a high coefficient of synchrony, high

coefficient of variation (standard deviation/mean) and periodicity (which could not be verified) must be present (Kelly 1994). With the synchrony measured within our study sites and observed before among other arctic species (Shaver and Kummerow 1992), we feel confident about using the mean number of floral buds and flowers of each population to represent interannual reproductive effort variability.

Factors associated with reproductive effort. To identify the variables that could predict the number of flower buds, flowers and fruits produced by *D. integrifolia* plants, multiple regressions were performed with data of each site using 10 independent variables (Table 2.3). With the Baker Lake dataset, our model shows that maximum thawing degree days accumulated 2 years before, raindays of the preceding summer season and maximum thawing degree days of June can predict at 88 % the flower production of *D. integrifolia* (Table 2.8). This relation is positive with the maximum thawing degree days accumulated in the growing season two years before and the number of raindays the preceding summer, but there is a negative relationship between flower production and thawing degree days of June. Tanquary data show that flower bud production can be explained at 69 % by accumulated maximum thawing degree-days in August of the preceding growing season (Table 2.9). No variable used in our analysis could explain the interannual variability of flower production in Tanquary as well as the variability of fruit production at both sites. Also, none of the winter variables used in our models had a significant influence on reproductive effort. Most plants did not show two years in a row of very high reproductive effort which suggests that there could also be an internal resource limitation that influences interannual variability of reproduction.

Synchrony of reproductive effort between low and high arctic sites. Figure 2.7 shows the interannual variation in mean flower bud numbers (a) and as deviations from the mean (b) (for each plant) during 1994-2005 at the two sites separated by almost 20 degrees of latitude. There seems to be a synchrony between the two sites in the variability of the mean number of buds produced per plant of *D. integrifolia,* especially when viewed as deviations from the mean (Figure 2.7 b) . This is noticeable especially for the peak production years of 2000 and 2003. Even if the multiple regressions showed

that the climatic variables influencing reproductive effort differed at Baker Lake and Tanquary, some more global environnemental factors may synchronise years of very high reproduction between these two distant sites.

2.6 DISCUSSION

2.6.1 Climate variability

Warmer than normal surface temperatures at Baker Lake and Eureka stations for most of our study period (Figure 2.2) are in line with the observed warming trend in most of the Arctic in recent decades (IPCC 2007, Serreze *et al.* 2000) and with Global Circulation Models (GCM) predicting that warming will be more severe at high latitudes (Maxwell 1992, ACIA 2005, Kaplan and New 2006). GCM's also indicate that warming will take place mostly in late autumn and winter (Chapman and Walsh 2007), a trend mainly apparent from Eureka weather station's dataset (Figure 2.2). Furthermore, models also predict an increase in climate variability in the Arctic (ACIA 2005). Interannual variability in surface temperatures is important at our sites, especially between consecutive winters and falls at Tanquary and falls and springs at Baker Lake (Table 2.4). Global warming coupled to high year to year or within season variability could lead to winter thaws and rain-on-snow events (Groisman *et al.* 2003). Such events may bring ice encapsulation, a disturbing process for the vegetation causing death from lack of oxygen (Crawford *et al.* 1994). Plant communities growing where snow cover is thin most of the winter, such as on exposed ridges (*e.g.*: Baker Lake site) and in polar semi-deserts (*e.g.*: Tanquary site), would be especially prone to this type of events.

While GCM forecast an increase in precipitation in the Arctic as part of global change (Serreze *et al.* 2000), summer precipitation anomalies for the 1990-2005 period do not show an increase or a decrease in precipitation totals or in number of wet days at our sites. It is possible that the time period considered was not long enough to show a trend or that an increase could have taken place in other seasons as only summer precipitations were considered in our study. According to the Arctic Climate Impact Assessment (2005), an 8 % increase in precipitations has taken place mainly in fall and winter over the last century in the Arctic. Despite the absence of trend in precipitations, we observed a high interannual variability of precipitations (rain) at both sites (Figure 2.3). The higher variability of precipitations in the Arctic than at temperate latitudes predicted

by the models (ACIA 2005) could accentuate years of high precipitations like the extreme totals recorded in the summers of 1997 and 2002 at Eureka station (Figure 2.3). Such events can contribute to a melting of the permafrost, and therefore an increase active layer depth, by a lowering of the water table resulting in a drying of the surface layer (Oberbauer and Dawson 1992, Woo and Winter 1993, Watson 1997). An increase of 12 % in frequency of heavy precipitation events has already been measured for Eurasian high latitudes in the last 50 years (Groisman *et al.* 2003). Indirect effects of those extreme precipitation events on vegetation are somewhat difficult to assess because melt of permafrost accompanied by a deepened active layer can also lead to greater N availability in a dry heath and a tussock tundra (Schimel *et al.* 2004) especially if combined to an increase in winter soil temperature (in snow covered areas) which leads to overwinter mineralization (Wijk *et al.* 2003). But at our exposed study sites, thin accumulations of snow probably do not allow high enough soil temperature for winter mineralization and there are more chances that extreme rain events would limit the growth of *Dryas integrifolia* by melting permafrost, lowering the water table and bringing drought for a longer period of the year.

During our study, summer temperatures showed smaller interannual variations than in other seasons (median of 1.05 °C a Baker Lake and 1.34 °C at Tanquary) but our results show that this variation was important enough to influence reproduction dynamics. Climate variability and the occurrence of extreme temperature and precipitation events will increase in further years with global change (ACIA 2005) but very little is known about the impact of such variability on growth and reproduction of arctic plants. Therefore, we recommend that long term experiments studying response of plants to climate change include manipulations simulating such variations and extreme events because most warming experiments measure the impact of a constant 1 to 3 °C increase with Open Top Chambers (OTC) over a few years (Marion *et al.* 1997) but do not simulate increased interannual and within season variability of summer temperatures and precipitations.

2.6.2 Interannual variations of phenology

Previous studies indicated a strong relationship between date of snowmelt, accumulated degree days and phenology in arctic and alpine ecosystems (Thòrhallsdòttir 1998, Molau 1993, 1997, Totland and Alatalo 2002, Dunne *et al.* 2003, Aerts *et al.* 2004). Snowmelt date had a large influence on flowering phenology of *Dryas integrifolia* at Baker Lake site but in the polar semi-desert (Tanquary site), budding and flowering timing relied mainly on degree-days accumulated in June. Because snowcover is generally thin or inexistant in the high artic zone, vegetation of polar semi-deserts might have the capacity to react more promptly and directly to temperature changes. A long term trend towards an earlier spring could mean that plants are active earlier in season when there is higher light intensity, resulting in a higher carbon sequestration over the whole summer and an increase in gross primary production, even if the length of the growing season stays the same (Euskirchen *et al.* 2006). We did not have biomass data from our sites to confirm that this was the case with *D. integrifolia* but in situ studies in Alaska, Sweden and Colorado have showed that with its wintergreen growth habit, *Dryas octopetala*, a closely related species, appears to be capable of expanding its period of growth in the fall and spring under warmer climate and longer growing season (Welker *et al.* 1997). With growing seasons expected to increase in length by 3 to 4 weeks in some parts of the Arctic within the next 50 years (Forland *et al.* 2004), there is a potential for a considerable increase in carbon sequestration by *D. integrifolia* in the arctic tundra.

While monitored only in *D. integrifolia* populations during our study, earlier flowering could probably be extrapolated to other tundra species of similar snow-poor exposed sites of the High Arctic. According to Molau *et al.* (2005) in a long-term study of flowering phenology in Swedish Lapland, the temporal sequence of species's first flowering dates is very constant among years which means that most tundra species bloom following the same order every year. If *D. integrifolia* advanced its flowering date by approximately 10 days since 1994 at Tanquary, it is very likely that other species showed the same response, especially early to mid-season flowering species which have rather constant TDD requirements for flowering among years. However, our results

could not be applied to later flowering species (for example: snowbed plants) that have more variable TDD at first flowering date mainly because of interannual variation in snowcover (Molau *et al.* 2005).

The relation between accumulated heat and fruiting phenology of *D. integrifolia* does not seem as direct as the one between TDD and flowering. At Baker Lake, although explained in part by June degree-days, fruiting date varied less than other phenophases and at Tanquary, none of the climatic variables used in the analysis was correlated to the variation of fruiting date. Internal cues might have an influence as environmental cues seldom stimulate the onset of fruit ripening and internal factors determine the rate of development (Larcher 2001). The absence of correlation between date of budding and date of fruiting tells us that onset of fruit maturation does not follow predictably onset of flowering as it does in some species (Ratcke et Lacey 1985). Although the onset of flowering seems unrelated to accumulated global radiation for most plants (Molau *et al.* 2005), this factor could have an influence on the onset of fruiting. Experiments in growth chambers with transplanted *Dryas* specimens could help controlling and identifying other external factors (ex.: photoperiod) acting as a trigger for fruit development.

The absence of correlation between TDD from the previous summer and date of flowering is not surprising in *D. integrifolia.* According to the extensive phenological study of Greenland plants by Sorensen (1941), wintering of the floral organs of *D. integrifolia* is always done at a well defined phase of development and their growth is often interrupted before the temperature conditions put an obstacle to its continuation. Floral buds are initiated in early spring of the previous growing season and development is stopped at a fixed stage (anthers formed and carpels slightly developped) no matter if the environmental conditions would allow more time to advance further the development of those floral buds. Therefore, pre-formed floral buds are always at the same stage when snow melts, year after year, and the bud break date depends on conditions of the current season and is independent from the conditions of the previous season. But in many species, this autonomous resting period is of short duration and a warmer fall

could have the effect of initiating opening of the preformed buds that were meant to open only the following spring, as it has been observed on the early flowering *Saxifraga oppositifolia* (Levasseur, non-published results) and on plants from Greenland transplanted in Denmark in the Fall (Sorensen 1941). Such events could lead to an exhaustion of the plant's resources and compromise its reproductive success in the long term.

2.6.3 Interannual variations of reproductive effort

As expected, our results show that environnemental cues were strongly involved in variations of number of buds and flowers of *Dryas integrifolia*. A combination of many factors is usually recognized to trigger floral induction (Heide 1994) and flower formation is often induced within a certain temperature threshold (Larcher 2001). One surprising finding of our study is that less floral buds and flowers were observed when June was warm at Baker Lake (Table 2.8). This result seems counter intuitive but Aerts *et al.* (2004) found similar results as experimental warming decreased flower production of *Rubus chamaemorus*, another Rosaceae. In addition, some species of the genus *Fragaria* (Rosaceae) are known to stop flowering at certain temperatures (Chabot 1978) and for many temperate zone species of the Rosaceae, vernalization (the process whereby flowering is promoted by a cold treatment) improves flowering (Michaels and Amasino 2000). Because very few additional buds are formed when a *Dryas* plant starts to flower, it could be thought that *Dryas* initiates more floral buds when spring is cooler because it would produce buds on a longer period (as long as temperatures are too cool to flower). However, our results show that there is no relation between the length of the budding phenophase and the total number of buds or flowers produced in a season. Even if the exact reason is unknown, our results show that *D. integrifolia* needs a period of cool weather (in June) to complete development of its preformed floral buds. It is already known that anticipated formation of organs in the Arctic is induced by low temperatures of the winter or early spring (flower buds are initiated in the spring of the previous year) (Sorensen 1941). Further investigations and laboratory experiments are needed to find out if there is a temperature threshold at which floral development is impaired. It is not surprising that accumulated TDD in June did not affect reproductive

effort of *D. integrifolia* at the high arctic site because temperatures are perhaps never high enough to interfere with the final development of the preformed floral buds at these latitudes.

At Baker Lake, raindays of the previous season were another factor associated with the number of floral buds observed on the plants. Because plants at this site are usually water limited from mid-season, it is possible that years with more raindays could have the potential to allow the growth of additional floral organs. These later formed floral organs would likely grow off a new shoot generation that could produce floral primordia later in the season, if conditions are favorable, and reach the same stage of development as those of the mother shoot before the wintering (Sorensen 1941). Thus, in dry years, only the mother shoot would initiate floral buds (early in the spring when it is not water limited), and in wet years, both mother shoots and the new generation of shoots would preform buds.

Finally, another factor linked with flower production at Baker Lake was TDD of the summer 2 years prior to flowering. This finding is quite surprising knowing that *D. integrifolia* initiates floral primordia only one season ahead (Sorensen 1941). However, because Sorensen (1941) did not use a SEM microscope, it would be possible that floral buds could be preformed more than one season in advance at a stage undistinguishable on a normal microscope, as observed on other arctic-alpine plants by Diggle (1997). In fact, Körner (1999) suggested that some plants could have 2 to 4 different cohorts of preformed buds that would all have the potential of flowering in favorable years. It is also known that plants from cold climates "over-initiate" flower buds and subsequently abort the surplus to allow the plant to take advantage of years with favorable conditions (Agren 1988, Körner 1999). For *D. integrifolia*, it is not clear if buds are aborted or if they could stay dormant until a favorable year. If the buds are preformed more than one season ahead and stay on the plant until a good season, it would explain why the conditions from two years ahead influence the number of floral buds and flowers observed. Another explanation of the influence of the season two years prior to flowering could relate to reserve accumulation. As the last months before

winter are being used to store reserves as starch in arctic plants (Sorensen 1941), the amount of assimilated matter stored that season could influence the energy available for floral buds prefomation the next spring and thus the number of flowers two summers later. Because flowers and seeds of arctic plants are not reduced in size as much as the vegetative parts of the plant, the accomplishment of the flowering shoot and fructification requires a comparatively large amount of concentrated energy (Sorensen 1941). Moreover, cushion plants have very low carbohydrate reserve and roots store less than shoots (Svoboda 1977). These reserves thus need to be as high as possible in the spring to allow for floral bud preformation (Sorensen 1941).

At Tanquary, heat accumulated in August of the previous summer was the only factor that influenced significantly variation of reproductive effort. Again, even if it is assumed that floral buds are initiated early in the spring the previous growing season, there seems to be some additional buds formed later in the summer, when conditions are favorable. Other unknown environnemental factors probably influence variation of reproductive effort at this site. Although we did not have data on accumulated global radiation, it would be surprising that it would play a role because Stenström and Molau (1998) observed that while radiation was the only factor influencing reproductive effort of *Saxifraga oppositifolia* and possibly some other true early evergreen, *Dryas octopetala* variation of reproductive effort was not synchronous with these species so different climatological factors were influencing this species.

At both sites, flower bud predation by insects and rodents was observed in the field and could have reduced the number of flowers and fruits produced and weakened the relationship between environmental variables and total number of fruits. Mature achenes are known as being a source of food for many rodents and bird (Aïken *et al.* 1999), indicating that once flower buds are initiatied, the proportion that will reach the fruit stage depends on variables (predation, etc.) other than the climatic variables we have used.

Our results indicate that interannual variation in number of flowers of *D. integrifolia* was synchronous within sites and to some extent, between our two distanced sites. It has been suggested that similar spatial linkage in timing of flowering (Post 2003) and large-scale synchrony of masting (Koenig and Knops 1998) could be due to large-scale climatic patterns like the Arctic Oscillation (Thompson and Wallace 1998, Kerr 1999, Moritz 2002). Eventhough our multiple regressions have shown that the factors influencing reproductive effort at the two sites are different, a global climatic pattern could have been governing different local weather conditions at our two sites and brought simultaneously favorable conditions related to a high flower production *(e.g.*: warm summer in the High Arctic and rainy summer in the Low Arctic).

2.6.4 Implications in context with Global Change

The synchronizing role of hemispheric climatic dynamics in the timing of life history in populations separated by hundreds of kilometers suggest that climate change has the potential to influence widely distributed populations and species simultaneously (Post and Stenseth 1999, Aanes *et al.* 2002, Blenkner and Hillebrand 2002, Post 2003). *Dryas integrifolia* is a major component of the vascular flora of the arctic tundra and understanding its reproduction dynamics gives an insight on changes to come on vast expanses of the tundra. For instance, warmer climate could increase seed production for *D. integrifolia* (Wookey *et al.* 1993), the main form of reproduction necessary to colonise the open landscapes of the High Arctic, in fellfields and forefield of retreating glaciers (Callaghan and Emanuelsson 1985). However, number of flowers produced could be reduced by warmer springs. Also, *D. integrifolia* and other plants of snow-free dry ecosystems whose active period ends by mid-summer and cessation of growth of the floral organs is autonomous (Sorensen 1941) could not take advantage of a longer season to preform floral primordia to a more advanced stage.

Pioneer plants like *D. integrifolia* are likely to be disadvantaged by an increase in soil mineralization. As demonstrated in recent studies, an increase in nutrients brings an increase in abundance of fast growing species (graminoids, deciduous shrubs,

herbaceous species) (Aerts *et al.* 2006) which are potential competitors for light and have proved to lead to a decrease of *Dryas octopetala* and *Saxifraga oppositifolia* (Robinson 1998). In a 15 years experience of Shaver *et al.* (2001), species composition changed dramatically from a mix of graminoids, evergreen, deciduous, and moss species to a dominance by a single deciduous shrub species (*Betula nana)* with nitrogen and phosphorus fertilization treatment in moist tundra. In warming experiments using Open Top Chambers, increased nitrogen mineralization of 70 % have been noted in three years (Aerts 2006) and in a study simulating climate warming with plastic dome greenhouses, plants had higher carbon, nitrogen and phosphorus pools after 5 years (Schmidt *et al.* 2002).

Drought brought about by a change in precipitation regime, severe heat or lowering of the water table would be detrimental for *Dryas*. In a polar semi-desert on Devon Island, *D. integrifolia* was missing on the driest crests where it can not tolerate hydric stress as much as *Saxifraga oppositifolia*, *Carex nardina* and *Salix arctica* (Svoboda 1977).

Changes in reproduction and vegetative growth of individual species will eventually bring changes in dominance of plant functional types and this may have large consequences for the amount of carbon fixed in Net Primary Production (Aerts *et al.* 2006, Aerts and Chapin 2000), the albedo and snow deposition (Sturm *et al.* 2001), the active layer (Watson *et al.* 1997), and the animal assemblage (Brown *et al.* 1997).

2.7 CONCLUSIONS

According to our study, *Dryas integrifolia* is showing a strong phenological response to climate variability and could take advantage of a longer growing season to complete seed maturation in the High Arctic and in the late snowmelt areas. However, flowering could be diminished if spring warms up too much and if competition for light with other plants arises with increased soil mineralization. The relation between climatic factors and reproductive effort are complex and influenced by more than one season. Indirect effects of temperature (increased mineralization, thicker active layer and drought) and precipitations (melt of permafrost, etc.) are difficult to assess. Flowering of *Dryas* has advanced considerably in the last 12 years at our high arctic site and other early flowering species likely advanced their flowering date at early snow free sites. From the synchrony of reproductive effort observed between the two populations separated by 20 degrees of latitude, we can expect that large scale climatic patterns will modify reproduction dynamics of tundra plants over wide regions.

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TABLE 2.1 Climate and vegetation characteristics (mean ± standard deviation) of the study sites,Tanquary Fiord and Baker Lake, Nunavut.

	Baker Lake (64°N)	Tanquary Fjord (81°N)
Climate		
Annual temperature (°C)*	-11.3 ± 1.5	-16.54 ± 1.08
July temperature (°C)*	11.4 ± 1.7	7.27 ± 1.74
January temperature(°C)*	-32.3 ± 3.4	-34.87 ± 3.76
Mean Thawing degree days*	967 ± 150	524 ± 118
Snowmelt date (julian)*	167 ± 11	160 ± 6
Annual precipitation		
Rain (mm)*	156.7 ± 24.7	33.43 ± 20.66
Snow (cm)*	120.35 ± 33.86	40.5 ± 11.9
Vegetation		
Bioclimatic subzone (Walker *et al.* 2005)	Erect dwarf-shrub tundra	Prostrate dwarf-shrub and herb tundra
% cover vascular plants	50-80 %	5-25 % (patchy)
Dominant vascular species of the site	*Dryas integrifolia* and *Cassiope tetragona*	*Dryas integrifolia* and *Saxifraga oppositifolia*
Mean vegetation height of the subzone	< 40 cm	5-10 cm

Climate data were obtained by Environment Canada Baker Lake A station for the Baker Lake site and by the automatic weather station of Qttinirpaaq National Park for the Tanquary site. Precipitation data used for Tanquary Fjord site are from the Environment Canada Eureka Station

**Means for 1990-2005*

TABLE 2.2 Independent variables used in multiple regressions of interannual variation of phenology (dates of peak budding and flowering and first fruiting) on climatic variables for 1990-2005 at the two study sites.

Independent variables	**Description**	**Mean ± SD for 1990-2005 Baker Lake**	**Mean ± SD for 1990-2005 Tanquary**
TDD max May	Maximum thawing degree-days accumulated in May	30.9 ± 19.4	22.6 ± 19.2
TDD max June	Maximum thawing degree-days accumulated in June	300 ± 88.2	207.6 ± 72.8
TDD max July	Maximum thawing degree-days accumulated in July	541 ± 70.2	306.8 ± 66.5
Snowmelt	First day of the year with no accumulation of snow on the ground (julian day)	167 ± 11 (June 16th)	160 ± 6 (June 9th)*
Raindays May-June	Total number of days with precipitations in May and June	18.8 ± 5.6	6.9 ± 7.5*
TDDmax -1	Maximum thawing degree-days accumulated during summer preceding flowering	1518.1 ± 199.8	783.8 ± 144.3

*Data from Eureka Station (data not available from micro-meteorological station in Tanquary)

TABLE 2.3 Independent variables used in the multiple regressions of interannual variation of reproductive effort (number of buds, flowers and fruits) on climatic variables for 1990-2005 at the two study sites.

Independent variables	Description	Mean ± SD for 1990-2005 Baker Lake	Mean ± SD for 1990-2005 Tanquary
TDD max June	Maximum thawing degree-days accumulated in June	300 ± 88.2	207.6 ± 72.8
TDD max July-1	Maximum thawing degree-days accumulated in July the summer preceding flowering	536.1 ± 65.9	306.8 ± 66.5
TDD max August –1	Maximum thawing degree-days accumulated in August the summer preceding flowering	449.3 ± 43.1	211.8 ± 61.1
TDD max september-1	Maximum thawing degree-days accumulated in September the summer preceding flowering	198.6± 59.8	21.3 ± 32.5
TDDmax-1 and TDDmax-2	Total maximum thawing degree-days accumulated one or two summers preceding flowering	1518.1 ± 199.8	783.8 ± 144.3
Raindays May-June	Number of days with at least 0.01 mm of rain in May and June	18.8 ± 5.6	6.9 ± 7.5*
Raindays-1	Total number of days with rain the summer preceding flowering	71.6 ± 10.5	30.4 ± 20.7
Freezing degree days	Accumulated degrees below threshold of -10 °C before there is a snow cover of at least 10 cm	156.6 ± 153	N/A Variable not used in analysis for this site
Tmin January	Minimum temperature in January	-35.6 ± 2.9	-38.2 ± 6.1

*Data from Eureka Station (data not available from micro-meteorological station in Tanquary)

TABLE 2.4 Year to year variability (median difference between mean temperatures of two consecutive years, Δ T) and range of mean temperatures (annual and seasonal) at the two study sites for 1990-2005.

	Baker Lake			Tanquary		
	Δ T (°C)	**Range(°C)**	n	**Δ T (°C)**	**Range(°C)**	n
Annual	1	-13.8 to -9.4	15	N/A	N/A	N/A
Winter	1.33	-33.8 to -27.1	15	2.89	-37.9 to -28.6	7
Spring	1.88	-20.2 to -13	15	0.92	-24.8 to -20.5	11
Summer	1.05	5.9 to 10.9	15	1.34	2.6 to 7.0	15
Fall	2.19	-10.3 to -3	15	1.76	-20.1 to -12.7	10

Winter = December, January, February, Spring = March, April, May, Summer = June, July, August, Fall = September, October, November.

TABLE 2.5 Multiple regression of median date of flowering (mean from flowering dates of 30 *Dryas integrifolia* plants) on climatic variables in Baker Lake between 1992-2005[1].
N : 13 Adjusted R^2 : 0.84

Variable	B ± SE	P
Intercept	139.73 ± 9.53	< 0.0001
Snowmelt	0.2742 ± 0.05	0.0007
TDDmax May	-0.0823 ± 0.0329	0.0336

[1]B = partial regression coefficient, SE = standard error. Note : Only the factors having a significant effect are presented ($p < 0.05$).

TABLE 2.6 Multiple regression of median date of flowering (mean from median flowering dates of 25 *Dryas integrifolia* plants) on climatic variables in Tanquary Fjord, Nunavut, between 1994-2005[1].
N : 11 Adjusted R^2: 0.51

Variable	B ± SE	P
Intercept	194.33 ± 4.49	< 0.0001
TDD Max June	-0.046	0.035

[1]B = partial regression coefficient, SE = standard error. Note : Only the factors having a significant effect are presented ($p < 0.05$).

TABLE 2.7 Multiple regression of first date of fruiting (mean from fruiting dates of 30 *Dryas integrifolia* plants) on climatic variables in Baker Lake between 1992-2005[1].
N : 13 Adjusted R^2 : 0.43

Variable	B ± SE	P
Intercept	195.67 ± 3.07	< 0.0001
TDD max June	-0.0242 ± 0.0094	0.0297

[1]B = partial regression coefficient, SE = standard error. Note : Only the factors having a significant effect are presented ($p < 0.05$).

TABLE 2.8 Multiple regression of mean number of flowers (mean from 30 *Dryas integrifolia* plants) on climatic variables in Baker Lake, Nunavut[1].
N : 13 Adjusted R^2 : 0.88

Variable	B ± SE	P
Intercept	-21.4107 ± 8.5	0.0359
TDD max -2	0.0130 ± 0.003	0.0065
TDD max June	-0.0332 ± 0.0097	0.0092
Raindays -1	0.3098 ± 0.0813	0.0052

[1]B = partial regression coefficient, SE = standard error. Note : Only the factors having a significant effect are presented ($p < 0.05$).

TABLE 2.9 Multiple regression of mean number of buds (mean from 25 *Dryas integrifolia* plants) on climatic variables at Tanquary Fjord, Nunavut[1].
N : 11 Adjusted R^2 : 0.69

Variable	B ± SE	P
Intercept	-12.55 ± 7.68	0.1366
TDD max August -1	0.1618 ± 0.0015	0.0015

[1]B = partial regression coefficient, SE = standard error. Note : Only the factors having a significant effect are presented ($p < 0.05$).

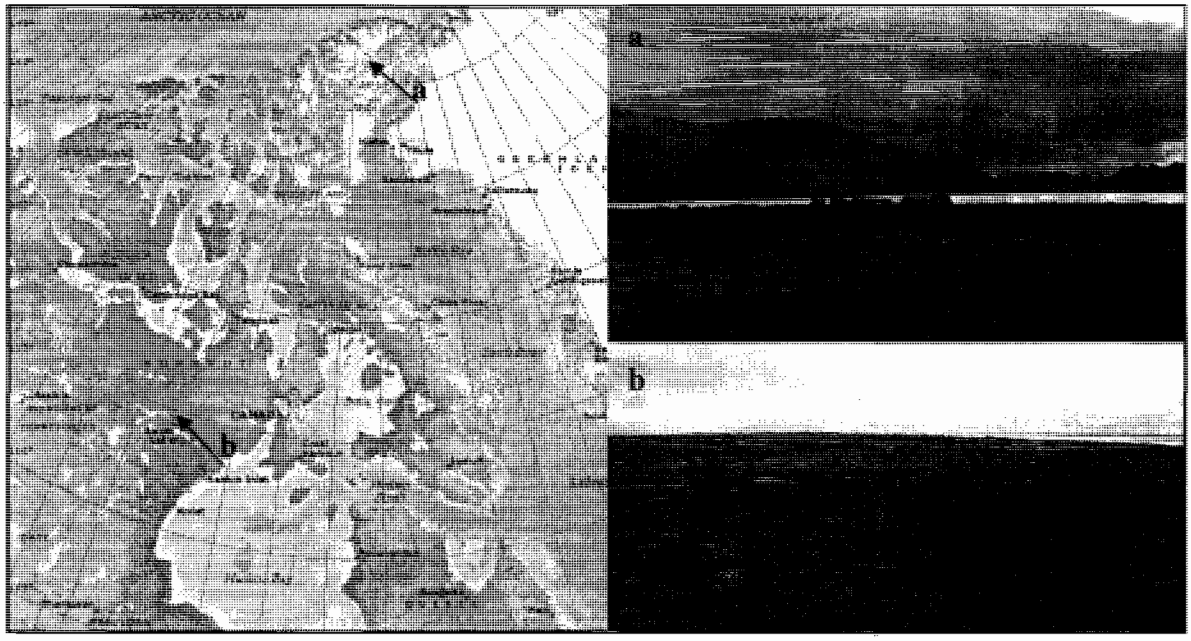

FIGURE 2.1 Location of the two study sites (modified from Microsoft Map Point) and picture of each site, a) Tanquary Fjord (81°N) and b) Baker Lake (64°N).

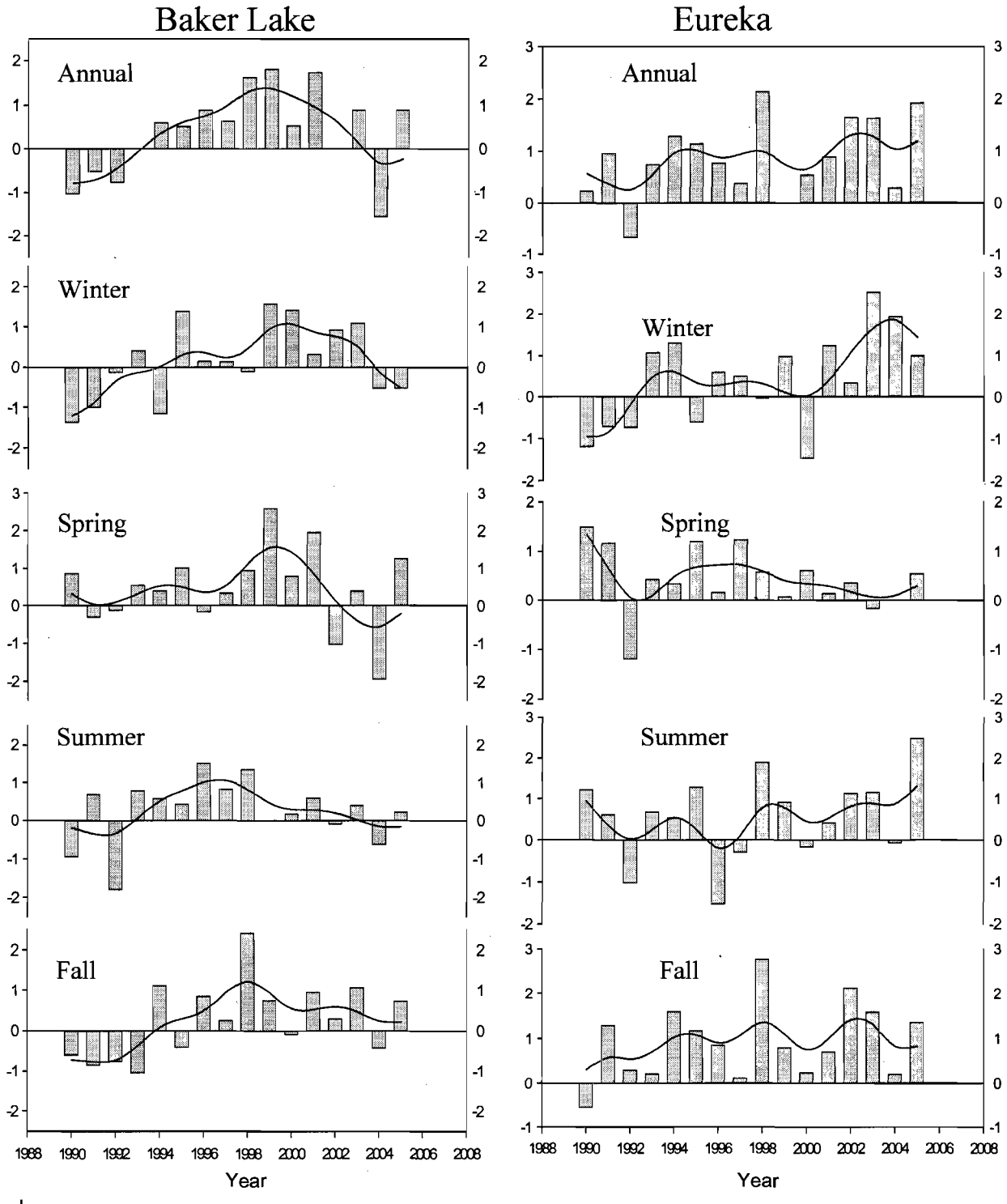

FIGURE 2.2 Annual and seasonal temperature anomalies (centered and reduced means) for 1990-2005 at Baker Lake and Eureka (Environment Canada meteorological stations) evaluated with respect to the 1971-2000 means. Smoothed line represents results from a Type 2 Hanning low-pass filter.
Winter = December, January, February; Spring = March, April, May; Summer = June, July, August; Fall = September, October, November.

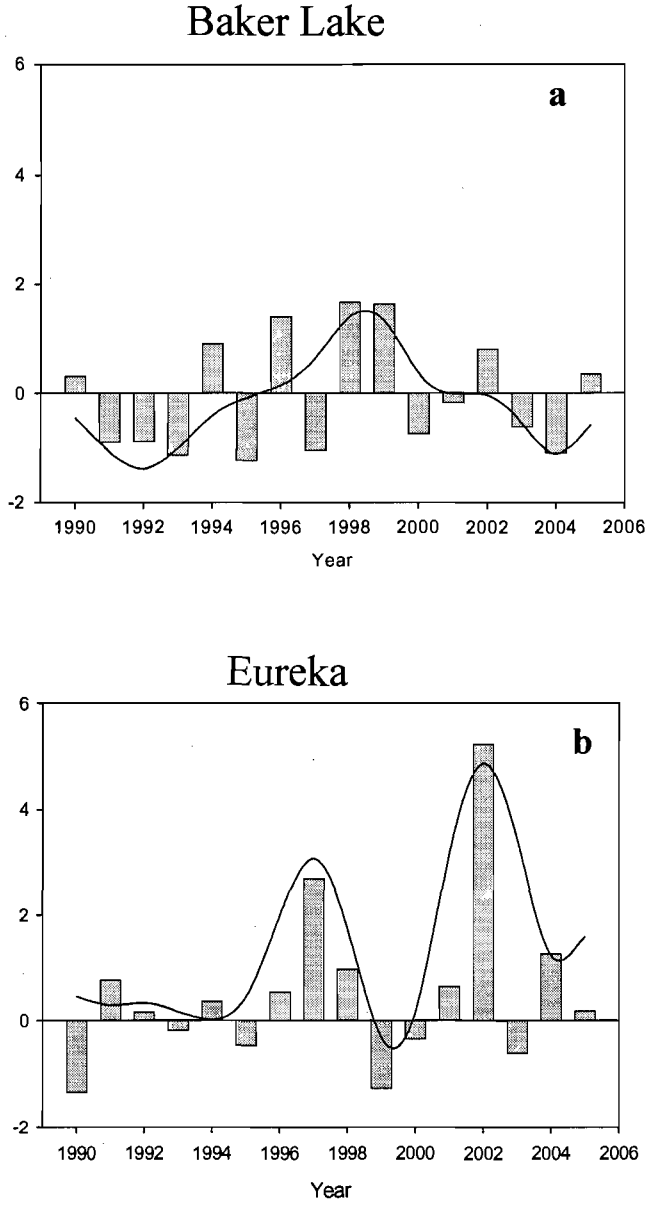

FIGURE 2.3 Liquid precipitation anomalies (centered and reduced means) for 1990-2005 at Baker Lake (a) and Eureka (b) (Environment Canada meteorological stations) evaluated with respect to the 1971-2000 means. Smoothed line represents results from a Type 2 Hanning low-pass filter.

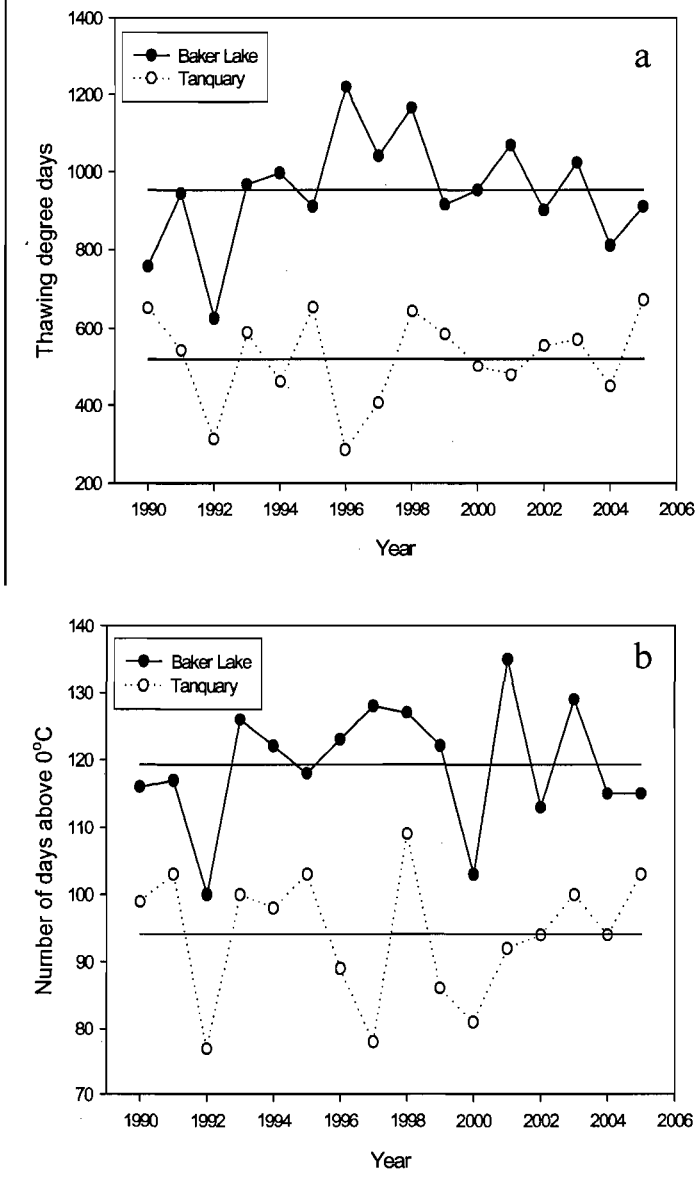

FIGURE 2.4 Mean thawing degree-days (a) and number of days with mean temperatures above 0°C (b) at Baker Lake and Tanquary Fjord.
Straight line represent mean for 1990-2005 period
(Baker Lake data from Environment Canada meteorological station and Tanquary data from automatic micrometeorology weather station of Quttinirpaaq National Park, Parks Canada).

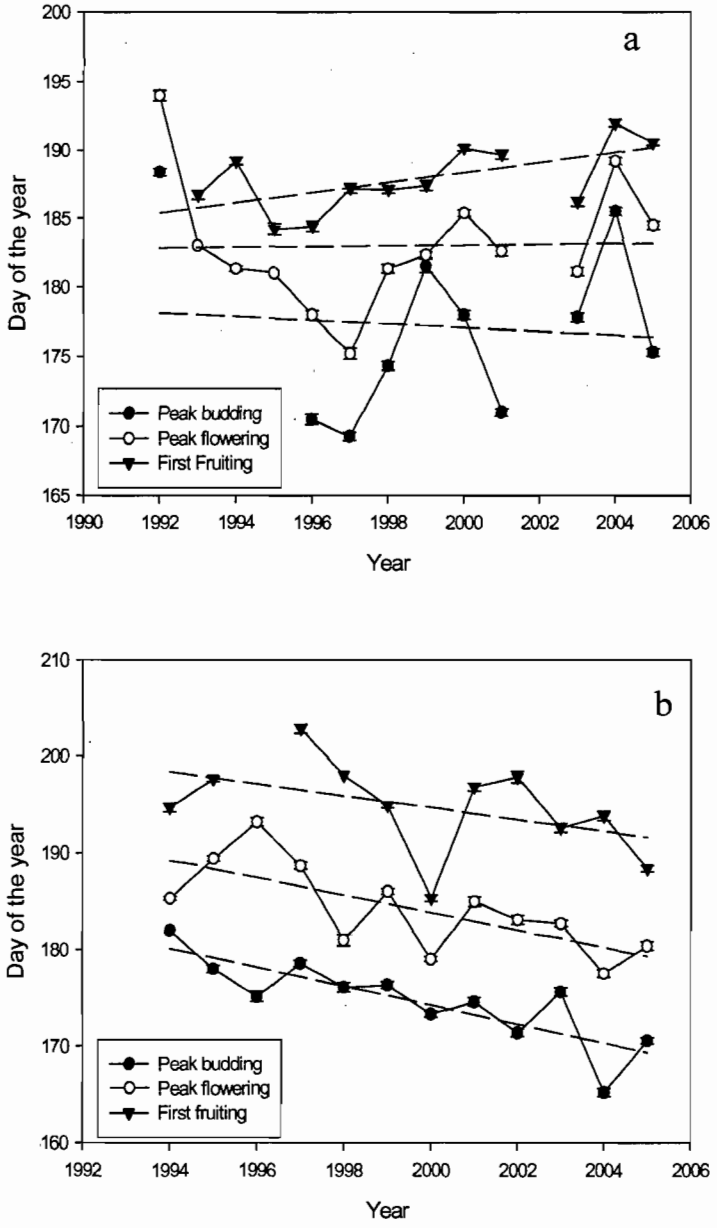

FIGURE 2.5 Interannual variation of dates of peak budding, peak flowering and first fruiting for *Dryas integrifolia*. Mean dates from 30 plants at Baker Lake (a) and 25 plants at Tanquary Fjord (b). Dashed lines represent least squares fit for each phenological phase.

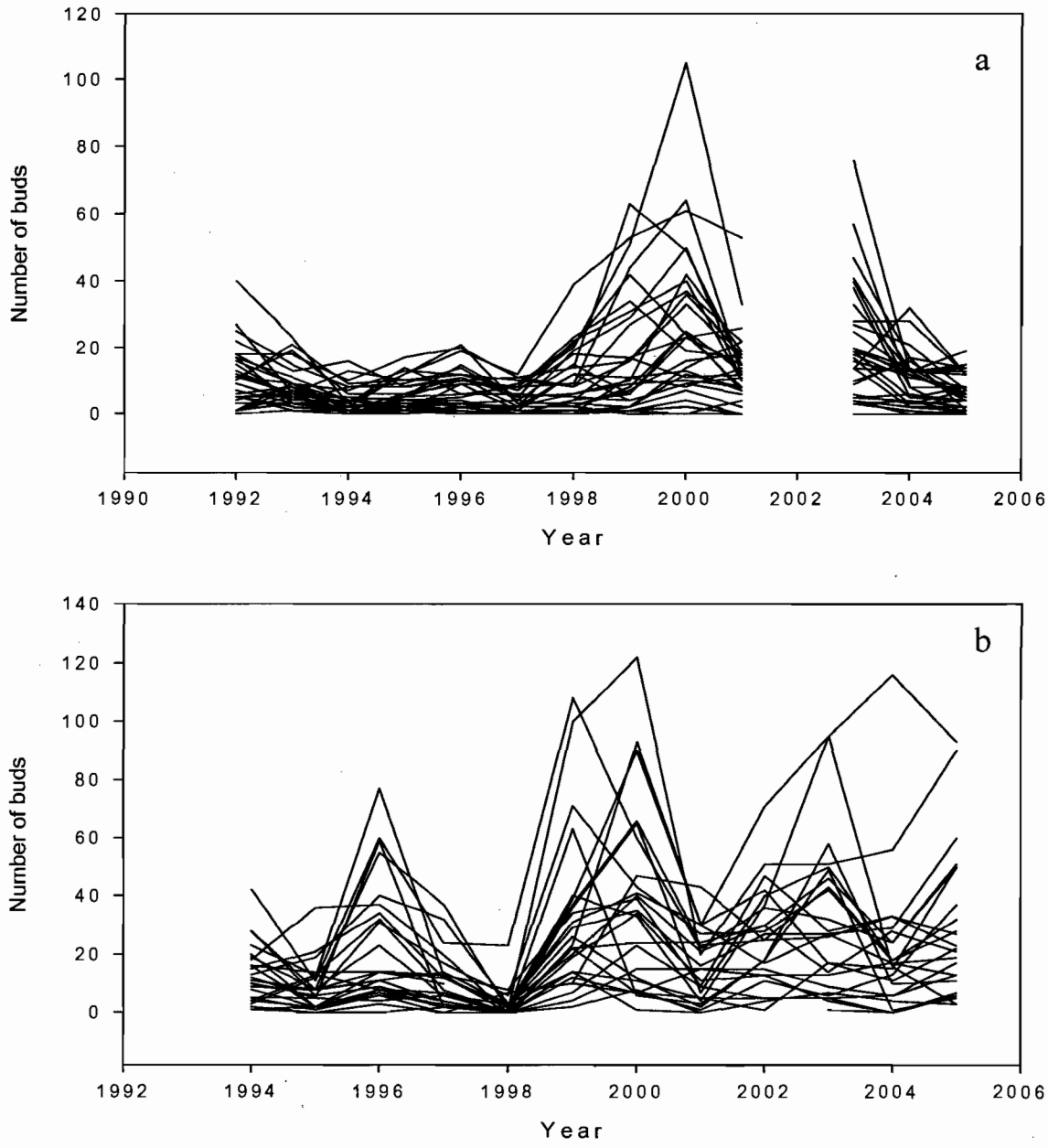

FIGURE 2.6 Floral budding dynamics (number of buds produced on each plant of *Dryas integrifolia* each year) between 1992-2005 at Baker Lake (a) and between 1994-2005 at Tanquary Fjord (b).

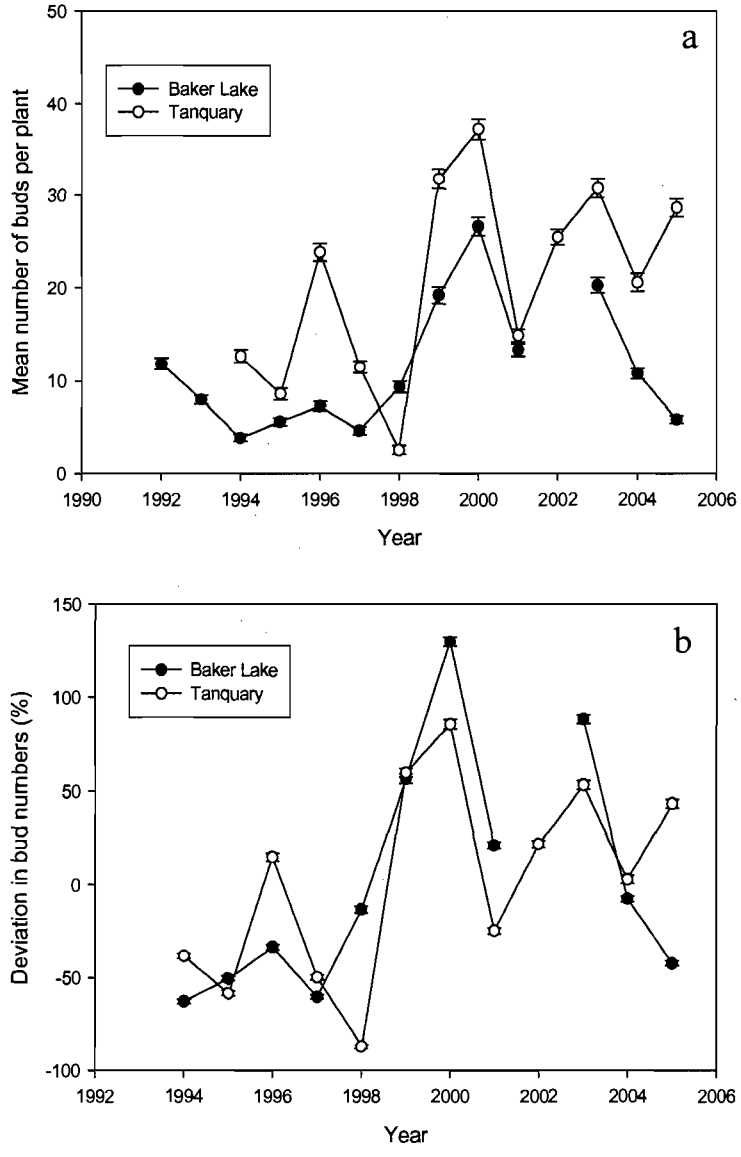

FIGURE 2.7 Mean number of floral buds from 1992 to 2005 (means ± SE) (a) and percent deviation from mean number of floral buds 1994-2005 (b) in permanently marked plants of *Dryas integrifolia* at Baker Lake (n = 30) and Tanquary (n = 25).

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ANNEXE 1

CARACTÉRISATION DU SITE ITEX DE BAKER LAKE

Les pages suivantes présentent des caractéristiques plus détaillées d'un des sites de recherche, soit le site ITEX (International Tundra Experiment) de Baker Lake (Figure A1.1). On y retrouve des mesures de micro-météorologie et une caractérisation de la végétation et du sol effectuées lors du travail de terrain qui s'est déroulé de la fin juin à la mi-août 2005.

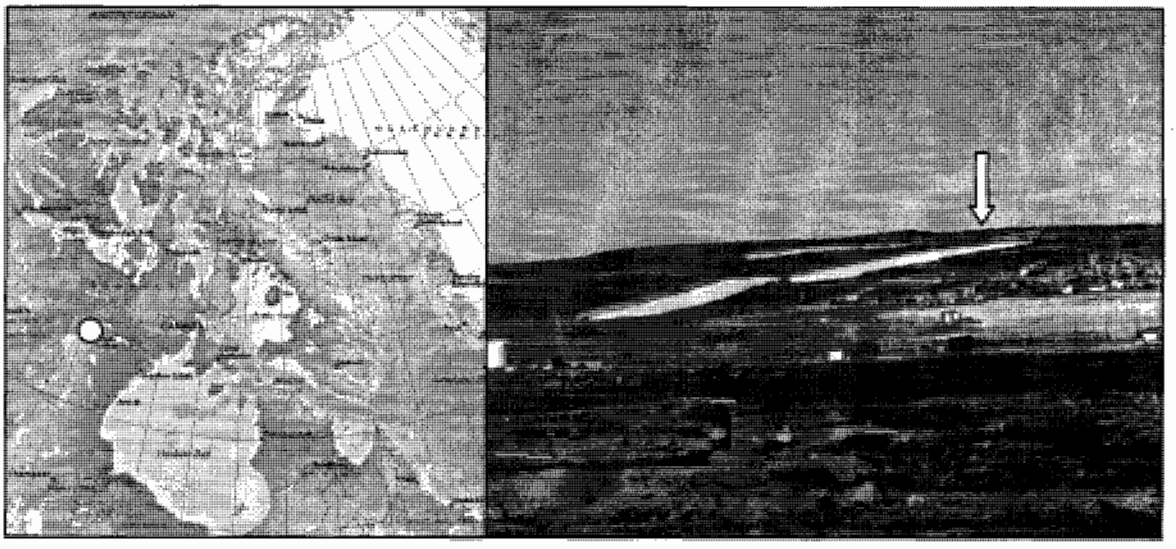

FIGURE A1.1 Localisation du site ITEX – « International Tundra Experiment » de Baker Lake, Nunavut (64°10'N, 95°30'W).

Ce site représente le seul site ITEX intérieur faisant partie de l'écozone arctique au Canada (tous les autres sont côtiers). On y retrouve un climat bas-arctique et le relief y est peu prononcé avec une pente généralement douce qui s'élève du lac (où se trouve le village) vers des crans rocheux granitiques au Nord. Le sol est composé de dépôts morainiques et plusieurs anciennes crêtes de plages forment des bourrelets graveleux parallèles au rivage (Figure A1.2a). Le site ITEX, situé sur le haut d'un cran rocheux du Bouclier Canadien, à environ 1 km du lac (Figure A1.1), possède un sol acide et bien drainé légèrement incliné vers le sud (Figure A1.2b). Un suivi phénologique a été initié

à ce site en 1992 par Josef Svoboda de University of Toronto et a été poursuivi jusqu'en 2005.

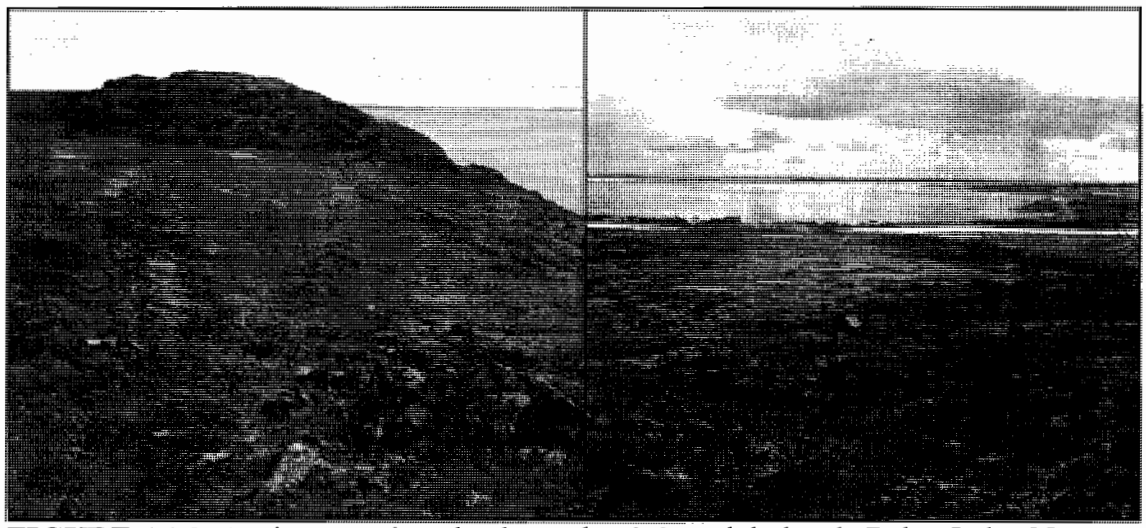

FIGURE A1.2 Anciennes crêtes de plages du côté nord du lac de Baker Lake, Nunavut (a) et vue vers le sud-ouest à partir du site ITEX (b).

MÉTHODES

Micro-météorologie

Des senseurs de type HOBO (modèle H8 à 4 senseurs) ont été utilisés pour prendre des mesures de température aux 10 minutes entre le 3 juillet et le 4 août 2005. Cinq senseurs ont été placés à 1 cm sous la surface de plants de *Dryas integrifolia* Vahl. du site ITEX. À partir de ces données, des moyennes journalières ont été calculées. Ces mesures visaient à vérifier la similitude entre les températures enregistrées par la station météorologique d'Environnement Canada « Baker Lake A » située à environ 1,5 km du site et pour laquelle nous avons des données à long terme (depuis 1945) et les températures réelles au niveau des plantes.

Caractérisation de la végétation du site ITEX de Baker Lake

Trente quadrats de 50 cm x 50 cm ont été disposés de façon aléatoire sur le site pour évaluer le recouvrement de la végétation et de certaines composantes abiotiques. Les plantes vasculaires étaient identifiées à l'espèce, à l'exception des Cypéracées (*Carex)* et des Graminées, identifiées seulement au genre étant donné que l'absence de floraison ou de fructification rendait leur identification difficile au moment de l'inventaire. La nomenclature des plantes vasculaires suit généralement Porsild et Cody (1980). Les lichens étaient identifiés au genre (Vitt *et al.* 1988) et le recouvrement des bryophytes a été évalué globalement. Le recouvrement de chaque taxon était noté en pourcentage et la moyenne de recouvrement était ensuite faite pour les 30 quadrats. Cette caractérisation avait pour but de faciliter la comparaison de nos résultats avec ceux d'autres sites.

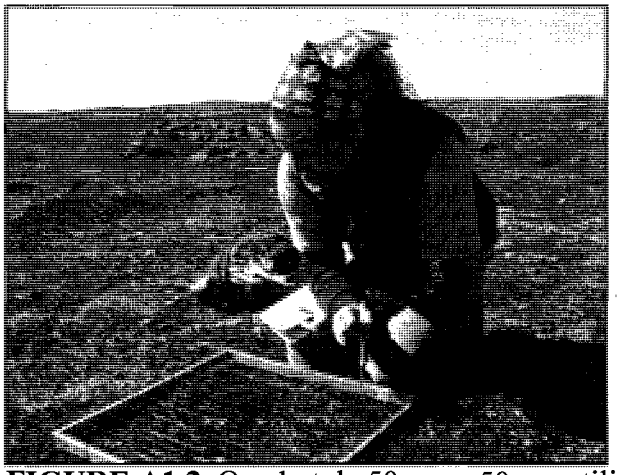

FIGURE A1.3 Quadrat de 50 cm x 50 cm utilisé sur le site.

Analyses de sol

Cinq échantillons de sol de 10 cm x 10 cm, sur 10 cm de profondeur, ont été prélevés au site ITEX sous des plants de *Dryas integrifolia*, *Empetrum nigrum* L., lichen et sol nu. Ces échantillons ont ensuite été séchés, tamisés à 2 mm, pesés et des analyses du pH, de la texture et du contenu en carbone, azote, phosphore et potassium ont été effectuées par le laboratoire du département de foresterie de l'Université Laval à Québec.

RÉSULTATS

Micro-météorologie

La Figure A1.4 présente la comparaison entre les températures moyennes journalières à 1,5 m du sol par la station d'Environnement Canada et celles enregistrées au niveau du sol (moyenne des 5 senseurs HOBO). Les températures dans les plantes étaient généralement un peu plus élevées qu'à 1,5 m, variant au cours du mois entre 3,4 et 27,2 °C par rapport à 2,6 et 25,8 °C à 1,5 m. L'intérieur des plantes était plus chaud que l'air ambiant durant les jours ensoleillés tandis que la différence entre la température du sol et celle à 1,5 m était presque inexistante et parfois négative par temps couvert. L'écart journalier des températures était aussi généralement plus élevé au niveau du sol qu'à 1,5 m, indiquant que le sol du site se réchauffait rapidement durant le jour mais avait une faible capacité à retenir la chaleur la nuit.

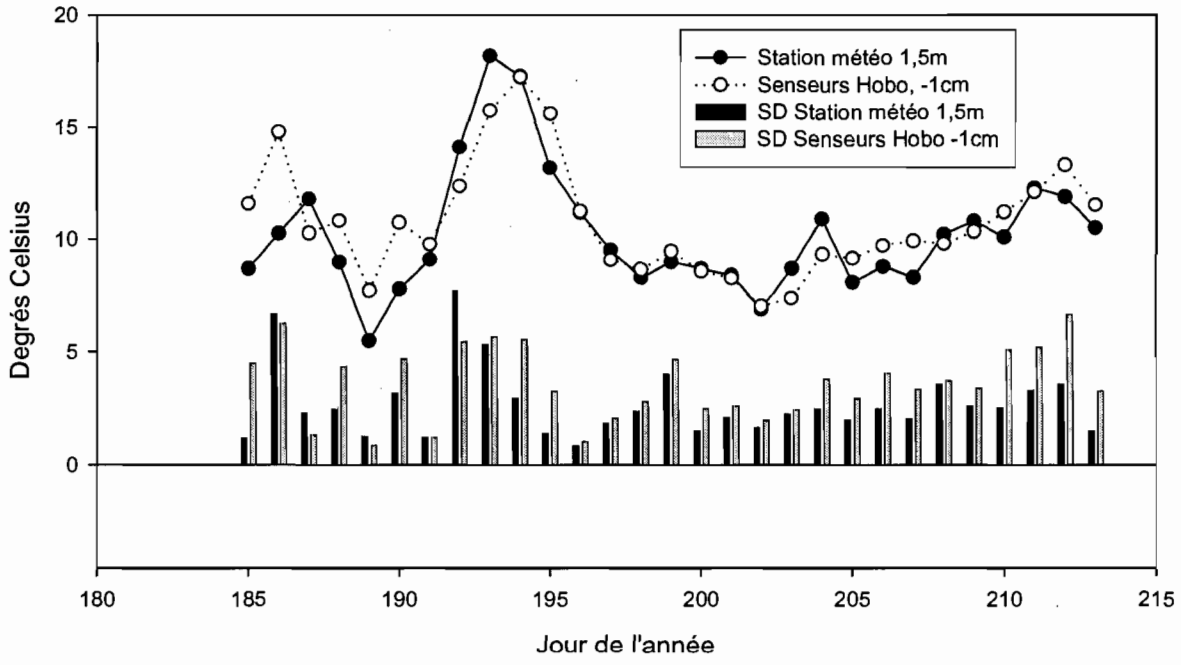

FIGURE A 1.4 Comparaison entre les températures moyennes journalières enregistrées à 1,5 m à la station d'Environnement Canada Baker Lake A et celles enregistrées par senseur HOBO (moyenne journalière des températures prises aux 10 minutes) à 1 cm à l'intérieur du sol sous des plants de *Dryas integrifolia* au site ITEX de Baker Lake durant juillet 2005. Les écarts-types pour chaque période de 24 heures sont présentés par le diagramme à barres.

Caractérisation de la végétation du site ITEX de Baker Lake

L'analyse des inventaires effectués au moyen des 30 quadrats démontre que les plantes vasculaires n'occupent que 41 % du site alors que les lichens et bryophytes en composent 49 % (Tableau A1.1). Il y a très peu de sol nu (4 %) et le recouvrement restant est partagé entre de la litière, de l'humus et de la croûte biologique. Les lichens du genre *Alectoria* ont un couvert très imposant (39 %) et semblent même croître par dessus les espèces vasculaires par endroits (Figure A1.5). *Dryas integrifolia* occupe 17 % du couvert et représente l'espèce vasculaire dominante du site, suivie de près par *Empetrum nigrum*, la seconde espèce dominante, avec 14 % du couvert. *Arctous rubra, Vaccinium vitis-idaea, Vaccinium uliginosum, Carex sp., Ledum decumbens* sont également présentes mais représentent seulement de 1 à 3 % de recouvrement chacune.

TABLEAU A1.1 Recouvrement (moyenne de 30 quadrats ± SE) des composantes abiotiques et biotiques présentes au site ITEX de Baker Lake, Nunavut.

Composante	Genre et/ou espèce	% Recouvrement (moyenne ± SE)
Sol nu		4,3 ± 0,5
Litière		2,8 ± 0,4
Humus		0,2 ± 0,1
Croûte biologique		1,9 ± 0,3
Lichens	*Alectoria sp.*	38,8 ± 0,8
	Dactylina sp.	0,7 ± 0,2
	Digitalis sp.	0,1 ± 0,1
	Cladina sp.	1,4 ± 0,7
	Cladonia sp.	0,3 ± 0,2
	Thamnolia sp.	3,5 ± 0,4
	Lichen non-identifié	2,6 ± 0,3
Bryophytes		1,7 ± 0,3
Plantes vasculaires	*Arctostaphylos sp.*	2,9 ± 0,5
	Astragalus alpinus	0,1 ± 0,1
	Carex sp.	1,7 ± 0,3
	Dryas integrifolia	16,5 ± 0,8
	Empetrum nigrum	13,5 ± 0,8
	Ledum decumbens	1,6 ± 0,4
	Oxytropis maydelliana	0,1 ± 0,2
	Saxifraga tricuspidata	0,1 ± 0,1
	Silena acaulis	0,3 ± 0,2
	Vaccinium uliginosum	2,2 ± 0,4
	Vaccinium vitis-idaea	2,9 ± 0,3

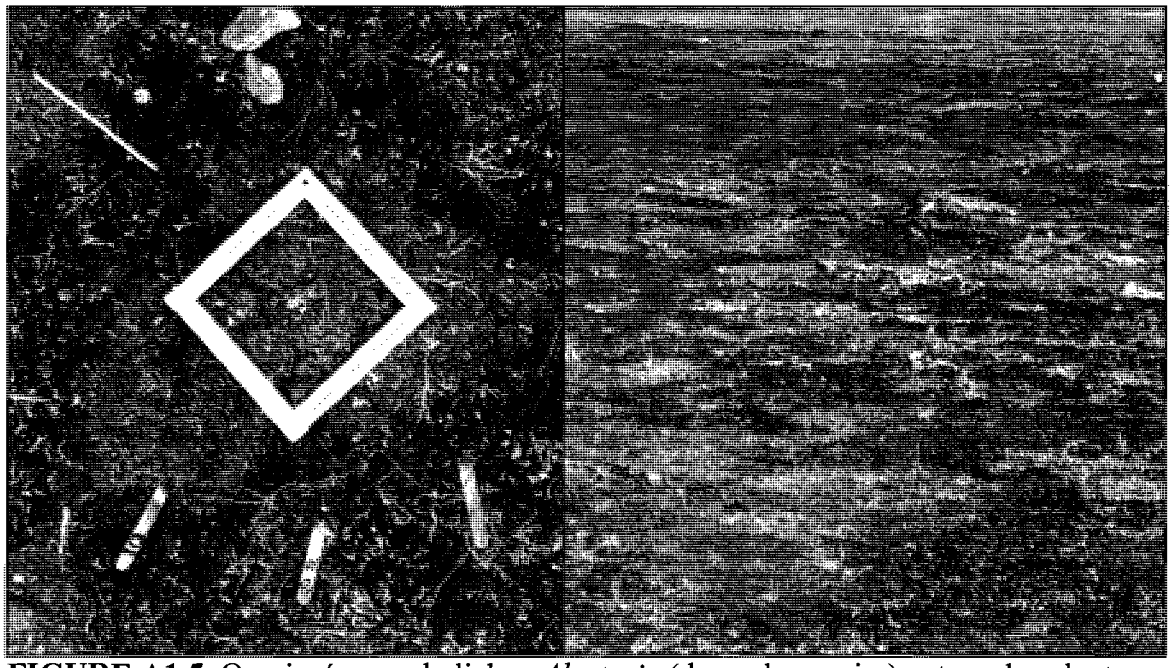

FIGURE A1.5 Omniprésence du lichen *Alectoria* (de couleur noire) autour des plants de *Dryas integrifolia* au site ITEX et dans les environs du site parmi *Empetrum nigrum* et *D. integrifolia.*

Analyses de sol

Le sol du site ITEX de Baker Lake contenait, avant tamisage, beaucoup de gravier grossier (> 3 cm). Après tamisage, il était de texture sableuse, contenait très peu d'azote (en moyenne 0,07 %), beaucoup de matière organique et était acide (pH moyen = 4,4). Les données de chacun des 5 échantillons sont présentées au Tableau A1.2.

TABLEAU A1.2 Caractéristiques du sol au site ITEX de Baker Lake, Nunavut, sous différentes plantes. Les échantillons ont été récoltés entre 0-10 cm de profondeur et analysés à partir de la fraction fine du sol (< 2 mm).

Variables	*Dryas integrifolia*	*Empetrum nigrum*	*Dryas integrifolia*	*Alectoria*	Sol nu
Texture					
% sable	89	91	92	93	90
% limon	4	3	3	2	2
% argile	7	6	5	5	8
Classe texturale	Sable	Sable	Sable	Sable	Sable
Carbone (%)	16,1	14,9	18,5	19,1	17,9
Azote (%)	0,12	0,06	0,04	0,05	0,09
pH	5,1	3,7	5,1	4,1	4,0
N/NH4+ (ppm)	5,1	4,6	2,1	3,3	4,2
N/NO3- (ppm)	1,9	1,3	1,4	1,3	2,0
Phosphore disp.(ppm)	31,6	10,5	24,5	30,3	24,0
Potassium disp. (ppm)	29,3	31,6	20,9	20,2	15,8

ANNEXE 2 :

EFFET D'UN RÉCHAUFFEMENT EXPÉRIMENTAL À L'AIDE DE SERRES OUVERTES « OPEN TOP CHAMBERS » (OTC) SUR LA PHÉNOLOGIE ET L'EFFORT DE REPRODUCTION DE *DRYAS INTEGRIFOLIA.*

Durant les travaux de terrain de l'été 2005 à Baker Lake, Nunavut, une expérience simulant un réchauffement climatique a été effectuée à l'aide de serres ouvertes « Open Top Chambers » (OTC) (Figure A2.1), non loin du site se suivi à long term ITEX – International Tundra Experiment.

MÉTHODES

Les OTC ont été construites selon les dimensions suggérées par Molau et Molgaard (1998). Un total de 14 parcelles contenant au moins un plant de *Dryas integrifolia* Vahl. a été réchauffé avec des OTC entre le 26 juin et le 30 juillet 2005 et 14 parcelles sans traitement ont été choisies comme témoins. Les stades phénologiques et le nombre de bourgeons, fleurs et fruits étaient répertoriés à tous les deux jours et la température à 1 cm sous la surface du sol était enregistrée au moyen de senseurs HOBO (modèle H8 à 4 senseurs ; 10 senseurs dans des OTC, 10 senseurs dans des parcelles témoins) à toutes les 10 minutes durant cette période.

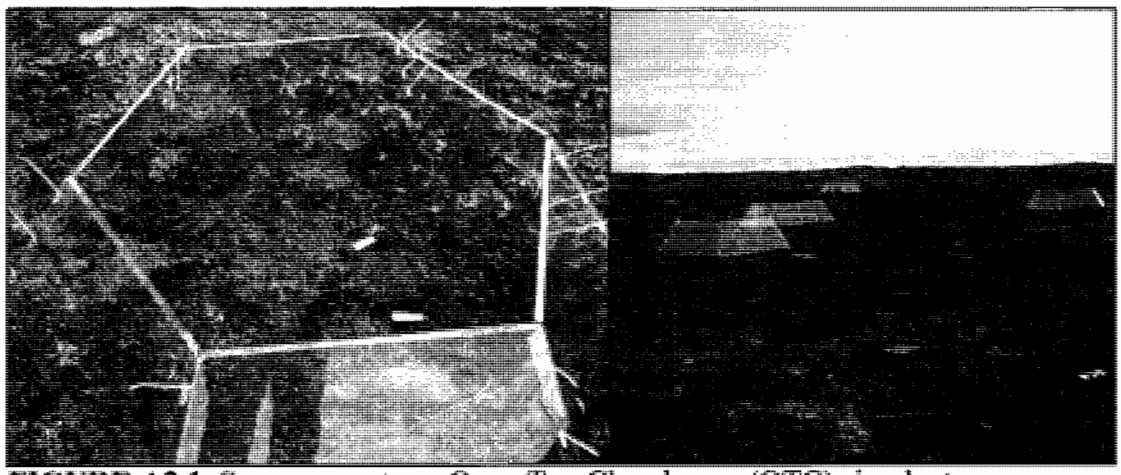

FIGURE A2.1 Serres ouvertes « Open Top Chambers » (OTC) simulant un réchauffement climatique sur les plants de *Dryas integrifolia* du site ITEX de Baker Lake, 62°N, Nunavut.

RÉSULTATS

Le réchauffement simulé par les OTC était en moyenne de 1 °C supérieur à la température enregistrée dans les parcelles témoins et ce, pour la période du 20 juin au 10 août 2005. La Figure A2.2 présente les moyennes mensuelles pour juillet 2005 dans les OTC et les parcelles témoins de même que la variation inter-annuelle des températures de juillet entre 1990 et 2005. On constate que l'écart inter-annuel des températures de juillet est grandement supérieur au 1 °C engendré par notre réchauffement expérimental. Bien qu'un réchauffement de l'ordre de 1 à 3 °C soit dans la norme pour une telle expérience (Marion *et al.*1997), la durée du traitement n'était probablement pas assez longue pour influencer la phénologie et l'effort de reproduction et cela découlait d'une livraison tardive des OTC sur le terrain.

Les dates de floraison et de fructification, les nombres moyens de bourgeons, de fleurs et de fruits, de même que le taux de prédation des fleurs et des fruits ne variaient pas significativement entre les parcelles réchauffées et non réchauffées. De plus, le pourcentage de bourgeons qui produisaient des graines semblait dépendre davantage de la prédation que de la température.

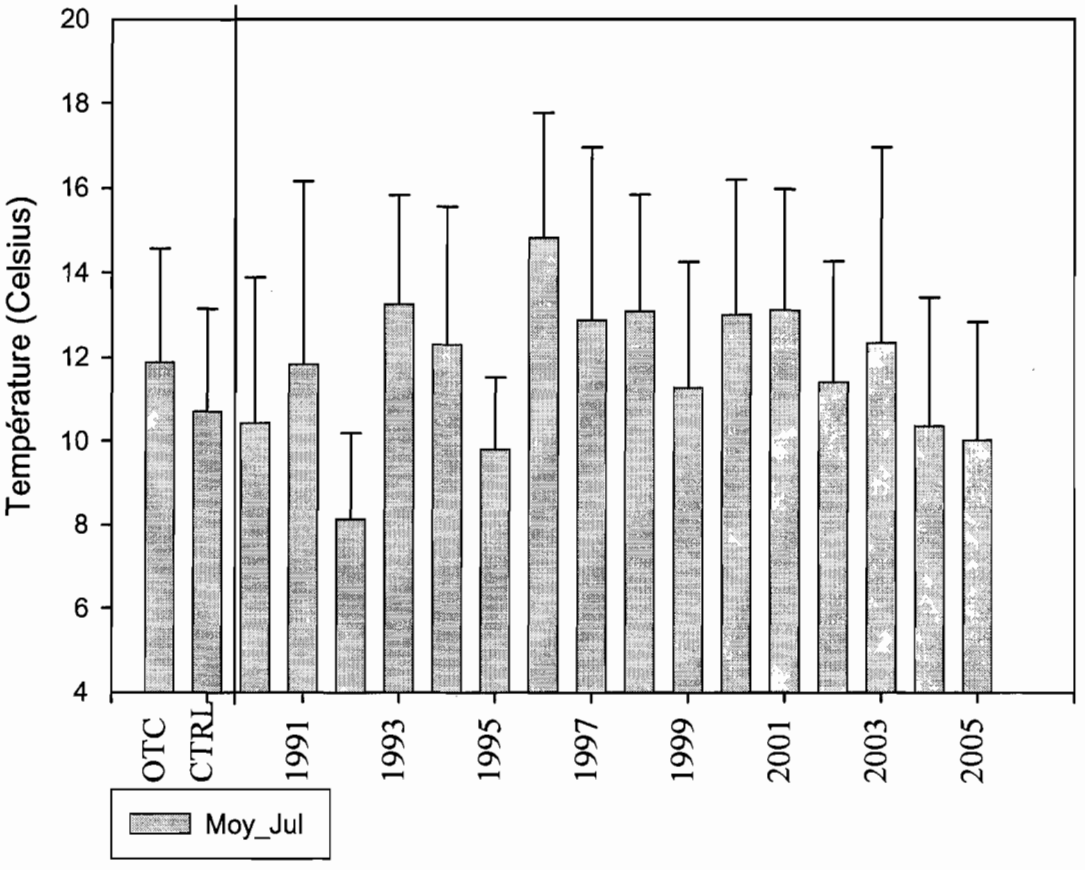

FIGURE A2.2 Températures moyennes et écarts-types des parcelles réchauffées (OTC) et témoins (CTRL) en Juillet 2005 et comparaison avec variabilité inter-annuelle des températures de surface pour Juillet (1990-2005).